Response of different plant functional types to environmental variability on Marion Island: Quantifying diurnal patterns over a seasonal cycle using the photochemical reflectance index

by

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Abstract

Marion Island forms part of the Prince Edward Island group, situated near the latitude of 47° South. Seasonal and temporal variability in climate on Marion Island has been described as muted, due to the thermal buffering of the surrounding ocean. This is thought in turn to lead to an extended growing season. However, empirical *in situ* measurements of net primary production (NPP), are lower than estimations based on annual temperature and precipitation.

The aim of this study was to explore which potentially limiting environmental factors exert control over photosynthetic behaviour at a range of sub-annual temporal scales, in order to better understand what limits production in plant functional types (PFTs) typical of Marion Island. The three main PFTs selected for study were lower plants, cushion plants and grasses.

Spectral reflectance sensors were used *in situ* to investigate the diurnal and seasonal patterns of physiological stress and inferred photosynthetic behaviour. The Photochemical Reflectance Index (PRI) is calculated from a ratio of reflected versus incoming light wavebands, that are influenced by a change in carotenoid ratios, indicating photosynthetic efficacy through the activity of the xanthophyll cycle. The xanthophyll cycle is closely linked to photosystem II and thus an important component of the non-photochemical quenching (NPQ) process that acts as a photo-protection mechanism.

PRI measurements require careful interpretation in the absence of any independent confirmatory measurements. Repeated ancillary measurements of leaf chlorophyll fluorescence and leaf chlorophyll content via independent instrumentation provided support for the PRI measurements as an indicator of physiological stress. This approach was also used to confirm that the point monitoring of individual canopies was representative of surrounding vegetation.

Contrary to the assumption that climate variability is muted, fine temporal scale monitoring revealed remarkably high temporal climate variability on Marion Island. Although seasons *sensu stricto* could not be clearly defined, a shift in climate can be seen between "winter" and "summer" months, most notably by a replacement of cold, calm days by warm, windy days. PRI data revealed that different PFTs (and to an extent, individual species) showed somewhat distinct optimum growing seasons, with the seasonal shift in climate affecting PFTs differently.

The three main PFTs showed distinct PRI patterns. Lower plants showed the deepest daily PRI depression, almost regardless of environmental conditions, confirming for the first time over an entire annual cycle their previously proposed low light adaptive

characteristics. Cushion plants only showed a midday PRI depression on days with high temperatures, revealing their optimal adaptation to cooler diurnal conditions. Grasses had the highest PRI values, responding positively on days with higher temperatures, and revealing their more efficient performance under warmer and brighter conditions, in distinct contrast to the other two PFTs.

Environmental drivers of stress varied significantly between PFTs. Lower plants were strongly influenced by moisture regimes and experienced significant stress during days of decreased habitat moisture levels. Cushion plants experienced less stress in colder temperatures, and responded positively to environmental variables that decreased canopy temperatures. Plant responses to changes in environmental variables were also clearly reflected in the seasonal PRI measurements. Grasses showed a decreases in stress during the "summer" months, while cushion plants experienced significantly more stress during the "summer" months. The lower plant species did not have a significant decrease or increase in PRI measurements between the different "seasons".

There is therefore no common or general driver of diurnal or seasonal stress response across different PFTs and species on Marion Island. This suggests that distinct PFTs would respond differentially as the climate regime continues to shift on Marion Island due to anthropogenic climate change. The in situ approach shows great promise for unlocking a deeper understanding of the environmental controls on this extraordinary ecosystem. The techniques described in this thesis would provide an extremely valuable set of tools to achieve this relatively inexpensively, while also providing a detailed picture of how this ecosystem is responding to climate change.

Opsomming

Marion-eiland vorm deel die Prince Edward-eiland groep, wat geleë is op die 40° suid breedtelyn. Variasie in klimaat op die eiland is voorheen beskryf as gedemp, as gevolg van die temperatuur buffer wat die omliggende suidelike oseaan bied. Verwagte plant produksie waardes, wat gebaseer is op temperatuur en reënval, is baie hoër as produksie waardes wat gemeet is op die eiland.

Tydens die studie is ondersoek ingestel om die daaglikse en seisoenale patrone van plant stres, produksie en fotosintese te ontdek en te bepaal wat hierdie patrone dryf en produksie op die eiland beperk. Daar is op drie hoof plant funktionele groepe gefokus: laerplante, kussingplante en grasse.

Afstandwaarneming stel mens in staat om ’n idee te kry van fotosintetiese aktiwiteite sonder om in direkte kontak te kom met die plant. Die fotochemiese-weerkaatsings indeks (FWI) kan ’n waardevolle indikator wees van plant fisiologiese verandering sowel as ander ekofisiolologiese aktiwiteite soos die zantofiel siklus. Die zantofiel siklus is gekoppel aan die tweede fotosisteem. Dit is ’n komponent van nie-fotochemiese onderdrukking proses wat dien as ’n fotobeskermmings meganisme. Hierdie proses kan die fotosintetiese aktiwiteit in ’n plant verminder.

Die ontplooiing van *in situ* sensors kan nuttig wees, met die aanvulling van klimaat en omgewings data, om plant produksie te bepaal. FWI meetings kan dikwels misleidend wees.. Heerhalende aanvullende meetings van chlorofil flourensie en blaar chlorofil inhoud, deur onafhanklinke instrumente, verskaf ondersteuning dat die meeting van individuele plantbedekking verteenwoordig is van die omligende plantegroei. Hierdie studie het gewys data FWI meetings ’n goeie aanwyser is van fisiologiese stres

Die hoë temporale resolusie metings, het ’n hoë variasie in klimaat gewys, veral wanneer die klimaat gekarakteriseer was op ’n kleiner tydskaal. Variasie in klimaat is dus nie so gedemp as wat voorheen beskryf is nie.

Die verskillende plant funksionele groepe het duidelike FWI patronne getoon. Laer plante het die diepste middag FWI depressie gehad, ongeag die omgewingstoestande. Kussingsplante het slegs ’n middag FWI depressie op dae met hoë temperature getoon. Grasse het die hoogste FWI waardes gehad en het positief gereageer op dae met verhoogde temperature.

Omgewingsdrywers van stress wissel aansienlik tussen verskillende plant funksionele groepe. Laerplante het beduidende stres ervaar gedurende dae van verminderde habitatvog.

Kussingsplante het minder stres in kouer temperature ervaar, en het positief gereageer op omgewingsveranderlikes wat plantbedekking temperature verlaag het.

Die plante se reaksies op veranderinge in omgewingsveranderlikes is weerspieël in die seisoenale FWI metings. Die grasse het gedurende die “somer” maande mider stres ervaar, terwyl kussingsplante gedurende die “somer” aansienlik meer stres ervaar het. Die laerplante het nie ’n beduidende afname of toename in FWI metings tussen die verskillende “seisoene” gehad nie. Daar is dus geen algemene omgewings drywer van daaglikse of seisoenale stres patrone oor verskillende plant funktionele groepe en spesies nie. Dit dui daarop dat verskillende plant funktionele groepe anders sal reageer soos die klimaatverandering voortgaan op Marion eilnd weens menslike klimaatsverandering.

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Abbreviations

Abreviations appear in alphabetical order and not in order as they appear in the document.

Fm	Maximum fluorescence
Fm’	Maximum fluorescence of an illuminated plant
Fo	Minimum fluorescence
Fo’	Minimum fluorescence of an illuminated plant
FOV	Field of View
FPAR	Photosynthetically Active Radiation
Fv/Fm	Potential maximum quantum yield of photosystem Ⅱ
FWI	Fotochemiese-Weerkaatsings indeks
GDD	Growing Degree Days
h	Height of sensor above canopy
HCRF	Hemispherical-conical Reflectance Facture
HFOV	Hemispherical Field of View
IRT	Infrared thermometer
kPa	Atmospheric pressure
LUE	Light Use Efficiency
NDVI	Normalized Difference Vegetation Index
NPP	Annual Primary Production
NPP_P	Annual Primary Production based on annual precipitation
NPP_T	Annual Net Primary Production based on annual air temperature
NPQ	Non-photochemical Quenching
P	Canopy Reflectance
PFTs	Plant Functional Types
P_i	Hemispherical sensor
Pp	Annual precipitation in mm
P_r	Downward facing sensor

PRI	Photochemical Reflectance Index
PS Ⅱ	Photosystem Ⅱ
psi PS Ⅱ	PS Ⅱ Yield
RH	Relative humidity
SRS	Spectral Reflectance Sensor
SVWC	Soil Volumetric Water Content
T	Annual air temperature in Celsius
T_{air}	Air temperature
T_{canopy}	Canopy temperature
T_{soil}	Soil temperature

1. An Introduction to Marion Island, Remote Sensing and Plant Production

1.1. Marion Island

Marion Island together with Prince Edward Island, form the Prince Edward Islands situated at 46° 54´ S, 37° 45´ E and 46° 38´ S, 37° 57´ E. Marion Island itself covers 290 km^2 in surface area. The Prince Edward Island group is located within the "Roaring 40s", aptly named due to the strong winds found south of the 40° line of latitude in the Southern Ocean. This group of islands has long been the focus of sub-Antarctic research. South African research teams have been permanently stationed on Marion Island since 1948, after Marion Island and Prince Edward Island were annexed by South Africa after the passing of the Prince Edward Island Act in 1948 (Smith and Mucina, 2006).

1.2. Climate

Marion Island falls within the sub-Antarctic region and has a hyper-oceanic climate (Smith and Steenkamp, 1990). The climate of Marion Island is therefore closely in equilibrium with the surrounding ocean, and is strongly influenced by frontal systems passing over it (Smith and Steenkamp, 1990). Marion Island's climate is characterized by high precipitation, high humidity, high cloud cover, and strong winds (Bergstrom and Chown, 1999). Precipitation in the form of snow, ice pellets, mist and rainfall is common, occurring on most days, with rain being the dominant form of precipitation found on the island. Annual precipitation is high (Schulze 1971). Meteorological data collected between 1960 and 2001 by the meteorological station installed on Marion Island indicates an increase in sunshine hours, with reduced rainfall. This has been accompanied by an increase in temperature together with a decrease in moisture on the island between this period (Mélice *et al.* 2003).

The air temperature and the sea temperature of the ocean surrounding Marion Island are tightly linked. This can be seen in the muted thermal fluctuations at both diurnal and seasonal scales found on the island (Schulze 1971). Due to the island's thermal buffering by the Southern Ocean, diurnal temperature differences are ±3° C and seasonal temperature differences are ±4.1° C (Schulze, 1971; Smith and Steenkamp, 1990). Diurnal temperature fluctuations lag behind the input energy of solar radiation. Regular cloud cover over the island restricts the amount of direct solar radiation reaching the surface of the island, with incoming solar radiation limited to only ±30% of the theoretical maximum at this latitude (Schulze, 1971).

Average wind speeds on Marion Island are measured at roughly 9 m/s, but gusts of more than 55 m/s are often measured (Smith and Steenkamp, 1990). It is to be noted that these measurements are taken near the base, which is situated within a wind shadow (colloquially known as "the Base bubble") and is therefore not representative of the climate over the entire island since spatial variation in climate can be significant across the island (Schulze, 1990).

1.3. Geology and topography

Marion Island has a volcanic origin, and currently two main types of lava rock flows can be found on the island. Previously glaciated Pleistocene grey lava can be found on the surface at certain places on the island, but elsewhere it is often covered by Holocene black lava or scoria. Both lava flow types are basaltic (Smith and Mucina, 2006).

The highest peak on the island is 1230 m above sea level and is found on the central highland interior. The highland interior slopes down to the coast to form low-lying shelves or plains. On the eastern and northern sides the coastal plains can stretch up to 5 km from the foot of the mountains to the coast. These planes rise gradually to 300 m above sea level. On the southern and western sides of the island the coastal plains barely rise above 100 m in altitude from sea level to the foot of the mountains (Smith and Mucina, 2006).

1.4. Vegetation and flora

Most sub-Antarctic islands are geologically very young, with Marion Island being only 500 000 years old. As a result of their young age and the fact that they were often glaciated during the Pleistocene Era, they are species poor (Boelhouwers and Meiklejohn, 2002). The most recent period of colonization was therefore only possible during the last 11 000 years (Boelhouwers and Meiklejohn, 2002).

Marion Island's plant cover is in the form of small ground plants and shrubs, with no trees or tall shrubs found on the island (Smith and Mucina, 2006). There are only 22 native vascular plant species on the island, with 18 introduced vascular plants. A high cryptogam diversity is found on the island with roughly 100 moss species, 100 lichen species and 42 liverwort species documented and recorded (Huntley, 1967; Smith and Mucina, 2006).

1.5. Remote Sensing of Photosynthesis

Remote sensing enables estimation of physiological activity without being in direct contact with the plant. This creates an opportunity to measure plant function from the scale of a single plant to large forest canopies. Remote sensing includes radiation measurements, gas-exchange measurements as well as measurements using spectrometric techniques (Filella *et al.* 1996). Spectrometric techniques include the use of thermal imagery, fluorescence and reflectance.

Remote sensing, together with ancillary techniques like gas-exchange, can be used to monitor temporal as well as spatial changes in primary production (Filella *et al.* 1996).

Remote sensing plays an important role in the modelling of plant production, the carbon cycle as well as other nutrient cycles (Malenovský *et al.* 2009). It has been used on both regional and global scales, however these have been at fairly large resolutions (Malenovský *et al.* 2009). Remote sensing using satellites have been commonly used for the past ±40 years with Land Remote Sensing Satellite (LANDSAT) being the first. LANDSAT opened the pathway for several spectro-radiometers placed on launched satellites enabling the measurement of narrow spectral wavebands to monitor vegetation function (Malenovský *et al.* 2009).

Photosynthetically active radiation (PAR) that is absorbed by the canopy has been used to remotely estimate the production of large plant canopies. Normalized Difference Vegetation Index (NDVI) and other vegetation indexes can be used to determine production over large areas. NDVI and other vegetation indexes use changes in the near infrared and the red wavelength spectrum. Satellite imagery can therefore be used to determine these vegetation indexes (Gamon, *et al.* 1997; Garbulsky *et al.* 2011).

With the use of remote sensing the opportunity to monitor and model production, photosynthesis and other canopy characteristics has arisen, but these model predictions do not always correlate with on the ground measurements (Malenovský *et al.* 2009; Harris et al. 2014). Although these measurements give a good indication of photosynthetic activity and production over large areas, discrepancies remain since the use of radiation for production can differ greatly between various species in an area and across different ecosystems (Garbulsky *et al.* 2011). Remote sensing models are therefore often used together with ground-based measurements in order to decrease discrepancies (Malenovský *et al.* 2009).

Close range remote sensing of the change in plant pigments can be a useful tool to measure plant production and photosynthesis on the ground. With the fairly recent development of measuring the change in xanthophyll pigments within the plant using two wavebands, the production of plant canopies can be measured in small areas (Gamon, *et al.* 1992; Gamon, *et al.* 1997; Garbulsky *et al.* 2011). This can be useful for addressing certain discrepancies of other approaches described above.

1.6. Photochemical Reflectance Index (PRI)

The Photochemical Reflectance Index (PRI) is a normalized difference index. It is often used to measure photosynthetic rates of plant canopies through remote sensing and can detect certain canopy photosynthetic characteristics (Gamon, *et al.* 1992; Barton and North, 2001). It

can also be used to model photosynthetic activity through means of light-use models (Gamon *et al.* 2015).

If a plant cannot use all the light that falls onto it for photosynthesis, the excess light energy may damage the photosynthetic apparatus of the plant found within the leaves (Gamon, *et al.* 1992; Gamon, *et al.* 1997; Garbulsky *et al.* 2011). The xanthophyll cycle helps to dissipate excess light energy in order to prevent the damaging of photosynthetic systems. During the xanthophyll cycle, epoxy groups are removed from epoxidised xanthophyll (violaxanthin) in order to generate de-epoxidised xanthophyll molecules (zeaxanthin), absorbing energy. The xanthophyll cycle is closely linked to photosystem Ⅱ (PS Ⅱ) and is a component of the non-photochemical quenching (NPQ) process (Gamon, *et al.* 1997; Garbulsky *et al.* 2011).

Through remote sensing, PRI can be used to monitor the xanthophyll cycle found within leaves. PRI measures changes within the carotenoid ratio of pigments found within leaves. The change in the carotenoid ratio of pigments leads to a change in the reflected waveband of 531 nm, however it has little or no effect on the reflected waveband of 570 nm. By comparing measured incoming and reflected wavebands (of both 531 nm and 570 nm), PRI can be used to track photosynthetic rates within the canopy of the plant. In low light environments, all light will be utilised in order to maximise photosynthesis and the PRI value will therefore be high. In environments where light intensities exceed the amount that can be used during photosynthesis, the xanthophyll cycle will increase and PRI values will be low or even negative (Barton and North, 2001).

Reductions in the photosynthetic rate of a plant due to environmental stresses other than light intensities, leads to an excess of light energy, and mechanisms for photo-protection will dissipate excess energy in the form of heat. It has been shown that a decrease in photosynthetic rates can be due to environmental stresses other than excessive light intensities (Filella *et al.* 1996).

PRI has been tested in various studies against other eco-physiological traits and has been shown to be a valuable indicator of photosynthetic rates as well as a proxy for other eco-physiological traits including light use efficiency, xanthophyll epoxidation, xanthophyll de-epoxidation, effective photochemical efficiency of PS Ⅱ, maximum photosynthetic rate, fluorescence steady state, non-photochemical quenching, ratio of carotenoid and chlorophyll content, electron transport rate, and stomatal conductance (Garbulsky *et al.* 2011; García-Plazaola *et al.* 2012; Rahimzadeh-Bajgiran *et al.* 2012; Zinnert *et al.* 2012; Harris *et al.* 2014; Magney *et al.* 2016).

PRI can be used to measure light use efficiency (LUE) and physiological responses to chronic environmental stresses on a small time scale (diurnal). Although it has been shown that there is a linear relationship between PRI and LUE, PRI is not directly related to LUE (Gamon *et al.* 1992; Filella *et al.* 1996; Guo and Trotter, 2006). PRI is related to the changes in the xanthophyll pigments which in turn relate to a change in the efficiency of electron transport within PS Ⅱ. However changes in the efficiency of electron transport in PS Ⅱ and the rate of CO_2 fixation will affect the LUE (Gamon *et al.* 1997; Guo and Trotter, 2006).

Various environmental conditions including air temperature, water availability, nutrient availability and wind have been shown to have an effect in the reflected 531 nm waveband. Environmental stresses therefore have been shown to effect PRI values on short timescales (Magney *et al.* 2016). PRI is influenced by rapid changes within the physiology of the plant and PRI measurements are best recorded at a fine time scale (≤1 min intervals) in order to represent an accurate idea of the diurnal physiological changes within the plant (Hilker *et al.* 2008; Magney *et al*. 2016).

On a seasonal timescale it is found that the PRI is influenced by the changing chlorophyll:carotenoid ratios and can be used as an indicator of carotenoid changes in response to environmental changes (García-Plazaola *et al.* 2012; Wong and Gamon, 2015). On a seasonal scale carotenoid ratio changes often reflect a response of physiological responses to environmental conditions such as seasonal transitions in response to seasonal climate changes (García-Plazaola *et al.* 2012; Wong and Gamon, 2015). It has been shown that on a seasonal scale PRI is more influenced by the changes in carotenoid levels (due to leaf development as well as chronic stress) than changes in the xanthophyll pigments (Filella *et al.* 1996; Garbulsky *et al.* 2011).

On different timescales PRI can therefore be used to measure photosynthetic efficiency as well as plant response to environmental stress. It is an effective method for monitoring photosynthetic rates and photosynthetic efficiency across a variety of environmental conditions (Garbulsky *et al.* 2011). PRI has regularly been used to determine LUE as well as photosynthetic performance in agricultural settings with a few studies being done on natural vegetation (Middleton *et al.* 2009; Garbulsky *et al.* 2011).

1.7. Plant production and photosynthesis on Marion Island

Annual temperature and precipitation data (Hijmans *et al.* 2005) were used to estimate net primary production of different Tundra systems across the globe based on the Lieth (1973) regression model. Primary production estimates showed that sub-Antarctic Islands have a

higher annual primary production than Northern Tundra biomes. This correlates with measured primary productions at different Tundra sites as compiled by the NASA Terrestrial Ecology Program (Figure 1.1 and 1.2) (Denissenko 2013; Esser 2013; Tieszen 2013).

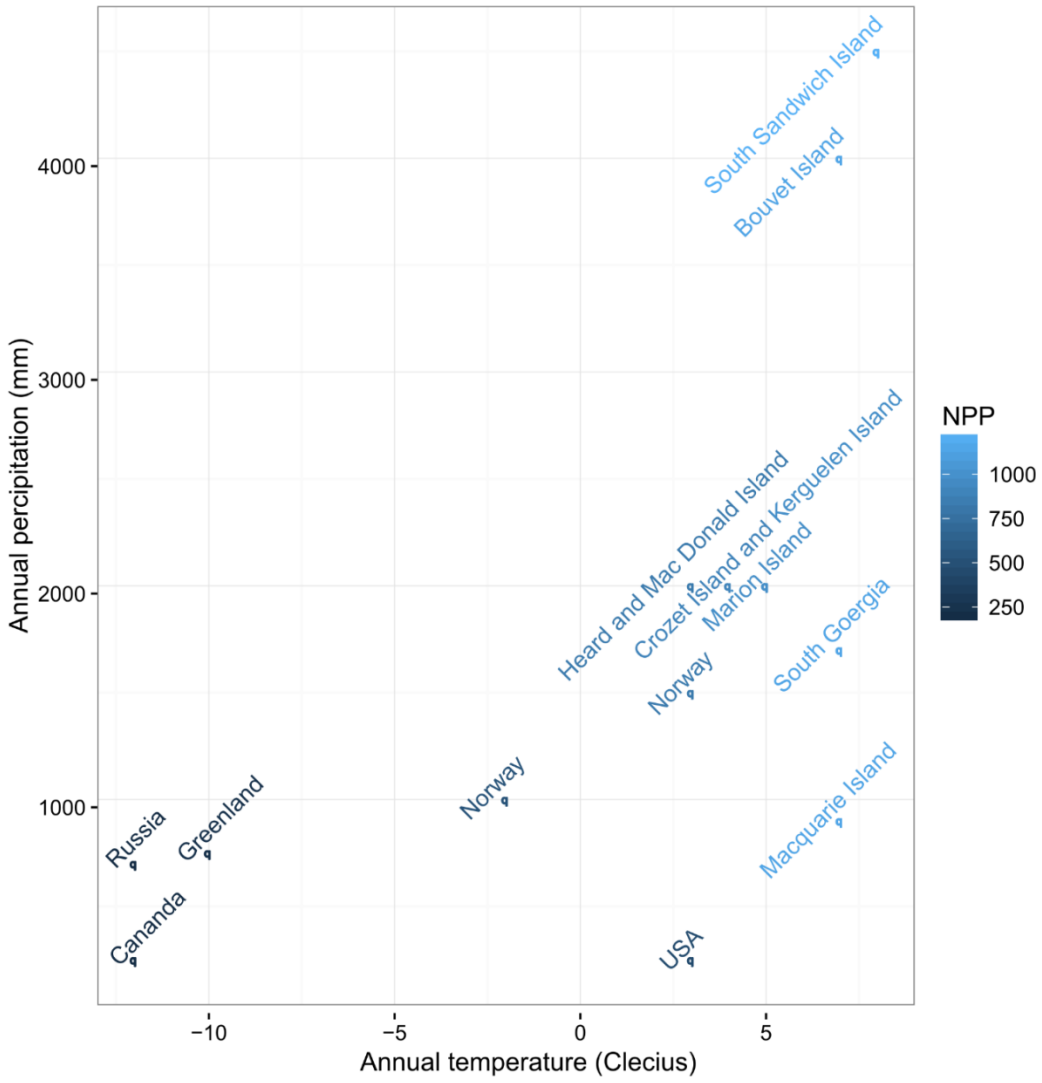

Figure 1.1 Annual primary production of Tundra type ecosystems based on their annual precipitation and temperature, as estimated by the Lieth (1973) Miami Model.

However, models such as the Miami Model (Lieth 1973) do not necessarily capture the influence of low seasonality on production, and they ignore solar radiation as a driver of NPP. High primary production measured on Marion Island, compared to Northern Tundra sites, is suggested to be a consequence of a long growing season (Smith 1987a), and a relatively slow but steady rate of production over this period. Due to the small variation in seasonal temperature and high moisture availability on the island, it is suggested that the growing season on Marion Island stretches from the middle of August to the middle of June (Smith, 1987a), a period therefore suggested to be ±10 months. This accords with the understanding of other sub-Antarctic islands, where growing seasons of a similar length have been reported (Smith, 1987a).

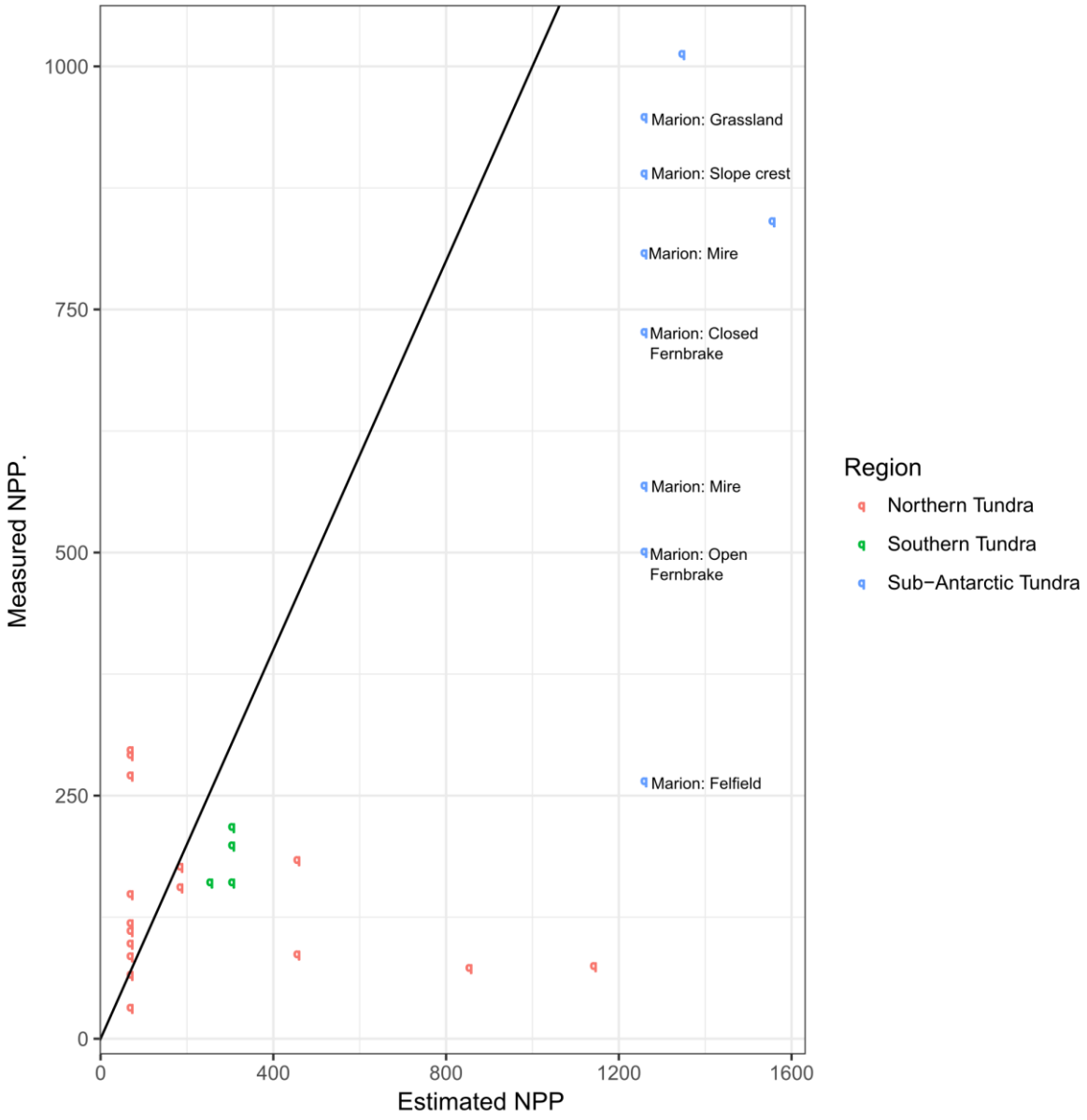

Figure 1.2 Measured annual primary production compared to estimated primary production based on the Lieth (1973) Miami Model. Colour coding according to general geographical location of Tundra sites where measurements were taken. Adline of expected relationship between measured and estimated NPP.

The lower annual primary production rates seen in the Northern Tundra vs sub-Antarctic biomes are likely a reflection of the colder annual temperatures and shorter growing season experienced in the Arctic, rather than the intrinsic ability of sub-Antarctic Tundra plant species to show higher growth rates. Growing seasons in Northern Tundra sites are much shorter (up to 6 months) than for sub-Antarctic Tundra communities. Higher primary production of sub-Antarctic Islands may therefore be due to the far longer growing season compared to the Northern Hemisphere, and not necessarily the inherent capability of sub-Antarctic plant communities to have high growth rates and productivity. Indeed, growth rates measured on Marion Island are between 0.9 and 3.1 $g.m^{-2}.day^{-1}$ (Smith 1987a, b). This is up to 50 to 30% lower than growth rates measured in the sub-Arctic, which have been measured to

be between 2.2 and 3.3 $g.m^{-2}.day^{1}$ (Denissenko 2013; Esser 2013; Tieszen 2013). The lower measured daily growth rates on Marion Island compared to the Arctic Tundra biomes supports the idea that air temperatures during the growing season on Marion Island are closer to optimal production levels for far longer periods of time compared to the Arctic, supporting slow and steady growth patterns (Hijmans *et al.* 2005). This idea has not been properly tested with modern *in-situ* monitoring equipment, and measurements of, for example, canopy temperature are virtually non-existent, and yet could be an important explanation of growth rate differentials.

Lieth's Miami Model has been shown to produce acceptable first approximation estimations of primary production over a variety of biomes and vegetation types (Lieth, 1973). Lieth's Miami Model estimation is based on the annual temperature and precipitation respectively, selecting the lowest estimation form either model (Equation 1.1) (Lieth, 1973). The following equations are from the Miami Model for estimating production Lieth (1973).

Equation 1.1 Lieth's Miami Model to estimate primary production based on annual precipitation and annual temperature

$$NPP = \min\left(NPP_T, NPP_P\right)$$

where NPP_T is the annual primary production estimation based on annual temperature (Equation 1.2) and NPP_P is the annual primary production estimation based on annual precipitation (Equation 1.3)

Equation 1.2 Annual primary production estimation based on annual temperature (T = annual temperature measured in Celsius)

$$NPP_T = 3000(1 + \exp(1.315 - 0.119 \times T))^{-1}$$

Equation 1.3 Annual primary production estimation based on annual precipitation (Pp = annual precipitation in mm)

$$NPP_P = 3000(1 - \exp(-0.000664 \times Pp))$$

The estimated annual primary production for Marion Island based on temperature and precipitation is ±990 and ±1960 $g.m^{-2}.y^{-1}$ respectively, suggesting that air temperature rather than water availability is a limiting factor. However, annual primary production measured on the island is between 226 and 949 $g.m^{-2}.y^{-1}$ (Smith, 1987a, b, c, d), which is well below the prediction of the Miami Model. This suggests that other environmental factors may well lower the rate of primary production on Marion Island below that which are potentially permitted by mean annual temperature.

Low radiation levels due to cloud cover on Marion Island has been suggested to strongly affect production rates of the island's flora (Smith 1987d). Cloud cover limits the duration

and intensity of incoming solar radiation (Smith 1987d). Smith (1987b) showed that plants found on Marion Island use incoming radiation as effectively as plants found in Tundra biomes in the Northern Hemisphere. Therefore, the low intensity and reduced duration of radiation levels are not sufficient to drive production to the limits permitted by mean annual temperature and is therefore hypothesized to be one of the main factors influencing primary production on the island.

High wind speeds are also hypothesized to be one of the main factors influencing primary production on sub-Antarctic Islands, but this factor is even less explored than light levels. Wind has been found to have a significant influence on the vegetation structure found on Marion Island (Smith and Steenkamp, 2001). It is also thought to influence plant function by depressing stomatal conductance due to the need to avoid freezing damage due to the chill factor (Smith and Steenkamp, 2001).

Different functional groups on the island are likely to show different proportional contributions to production on Marion Island. Lower plant species (bryophytes and liverworts) in Tundra biomes are found to be strongly influenced by water regimes (Russell, 1990). Bryophyte production rates can be high in low light environments due to their shade adapted physiology. In environments where there are not a high seasonal variability in climate, it has been found that bryophytes are less adaptive to a changing light and temperature environment (Russell, 1990).

Production of vascular plants can be limited by light and temperature, with production being lower than in bryophytes in low light environments (Russell, 1990). Grass species on Marion Island have been found to have a broad optimum temperature spectrum and can maintain high levels of production and photosynthesis at a wide range of air temperatures (Pammenter *et al.* 1986).

It is therefore likely that distinct plant functional types (PFTs) are differentially sensitive to the wide range of abiotic factors limiting growth and productivity on Marion Island. However, despite a few detailed studies, there is no comprehensive study that explores the role of these factors *in situ* on the range of PFTs on Marion Island.

Meteorological data collected on the island shows an increase in sunshine hours and temperatures with reduced rainfall between 1960 and 2001. This has had a direct impact on species distribution and productivity on the island (le Roux and McGeoch, 2008b). A better understanding of production in response to diurnal and seasonal climate variability in a

variety of PFTs will contribute to predicting future production on the island especially in terms of how it will be affected by climate change.

1.8. Aims and Objectives

With high temporal resolution measurements of canopy temperature, PRI as well as other environmental variables, it is possible to develop a deeper understanding of the plant physiological responses to a changing environmental climate. This will give an insight into whether the primary production measured on the island is a reflection of stable seasonal climate conditions or whether environmental variability on different timescales has a greater influence on plant photosynthesis and production than previously thought. Different functional groups found on the island may respond differently to different environmental variables and may have different environmental variables limiting production.

In situ measurements of various vegetation indexes (PRI and canopy temperature) will help to gain a better understanding of how extreme sub-Antarctic weather conditions will affect plant physiological stress, photosynthetic performance, and canopy growth and status.

This study will investigate the seasonal and diurnal patterns of different plant functional groups with a primary reliance on the PRI. The study aims to:

- Describe the seasonal patterns in key environmental variables over an annual cycle under extreme sub-Antarctic weather conditions.
- Demonstrate the efficiency of a close-range remote monitoring system of canopy temperature, photochemical reflectance, and relevant environmental variables, under extreme sub-Antarctic weather conditions.
- Describe the diurnal and seasonal patterns of physiological stress, photosynthetic performance, and canopy growth and status of three important plant functional types under extreme sub-Antarctic weather conditions.
- Determine the role of diurnal drivers (temperature, wind, precipitation, humidity, solar radiation and altitude) of physiological stress in three important plant functional types.
- Determine the role of seasonal drivers (soil water, temperature, solar radiation and day length) of physiological stress and photosynthetic performance in three important plant functional types.

2. Methods

2.1. Study species

Six focal species were selected for this study, representing three distinct functional groups, namely: Grasses (graminoids), cushion plants (herbaceous plants) and lower plants (bryophytes and liverworts). Much previous work suggests that these functional types should display distinct diurnal and seasonal photosynthetic and production performance. Within the selected species group there was a combination of invasive and endemic species to Marion Island, as listed in Table 2.1.

Table 2.1 Focal species growth form/habitat and life form.

Species name	Life form	Growth form/ habitat
Azorella selaga	Vascular	Cushion plant
Sagina procumbus	Vascular	Cushion plant
Agrostis magellanica	Vascular	Graminoid
Agrostis stolonifera	Vascular	Graminoid
Racometrium lanuginosum	Bryophyte	Tuft moss
Syzigiella colorata	Bryophyte	Tuft moss

Study sites

Three study sites were chosen at the same altitude of 30 – 50 m above sea level. The study sites are depicted in Table 2.2 (Smith and Steenkamp, 2001; Smith *et al*. 2001).

Sites were selected to ensure that a monoculture canopy of species pairs in the same functional type were present (ie each site monitored a single PFT). A movable arm allowed the critical radiation sensors to be switched between canopies for two week periods through the year of sampling. This ensured that both species at each station were monitored during all seasons The altitude and the co-ordinates of the three sites were determined using a Garmin Legend HCx GPS (Figure 2.2).

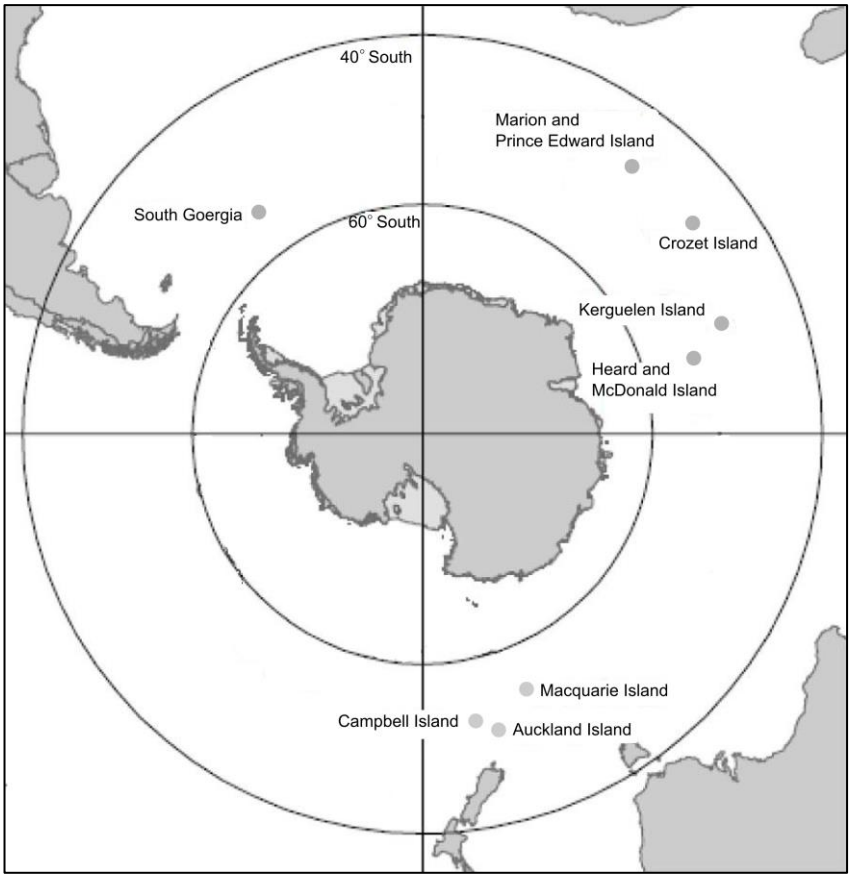

Figure 2.1 Map of Sub-Antarctic islands including Marion Island in the Southern Ocean. Adapted from Williams (2013).

Figure 2.2 Map of (A) Marion Island with Marion Research Base and (B) site selection close to Marion Research base. Mercator World Projection used.

Table 2.2 Pictures of the three study sites and the focal species found at each site.

Site number	Photo of study site	Focal species found at site
Site 1		*A. selaga*
		*S. procumbus*
Site 2		*A. magellanica*
		*A. stolonifera*
Site 3		*R. lanuginosum*
		*S. colorata*

2.2. Spectral reflectance sensor (SRS) setup

The PRI of the selected plant species canopies was continually measured at 1 min intervals for the period of one year at fixed locations using a spectral reflectance sensor (SRS), manufactured by Decagon Devices (Gamon *et al*. 2015; Magney *et al.* 2016).

PRI sensors consist out of photodiodes with interference filters that are sensitive to wavelengths at 531 nm and 570 nm and have a 10 nm of full width at half maximum band widths. Simultaneous measurements of P_r and P_i (reflected ind incoming) by the hemispherical and downward facing SRS sensors, ensure that the hemispherical-conical reflectance fraction (HCRF) was measured.

SRS sensors compute the PRI by measuring canopy reflectance (P) using specific wavelengths, via the following equation:

Equation 2.1 PRI calculation

$$PRI = \frac{P_{531} - P_{570}}{P_{531} + P_{570}}$$

where P_{531} and P_{570} are the percentage of reflectance at the specific wavelengths of 531 and 570 nm respectfully (Gamon *et al.* 1992; Penuelas *et al*. 1995).

The SRS sensors are able to measure the PRI by sensing the radiation scattered into the field of view (FOV) of 36° of a downward facing sensor (from here on referred to as P_r) that is positioned above the canopy of a vegetation community. The P_r sensor was accompanied by an upward facing hemispherical sensor (from here on referred to as P_i) positioned with a hemispherical field of view (HFOV) of 180°. The P_i sensor measured the incoming radiation.

The following equation was used to determine the total area that fell within the field of view of the downward facing sensor (with 18° half view):

Equation 2.2 Determining FOV as determined by the manufactures (Degacon Devices).

$$Area\ in\ FOV = 2 \times (\tan(18) \times h)$$

where h is the height of the sensor above the canopy.

The height of the sensors above the canopy was slightly different at each station in order to ensure that only the canopy of a monoculture species fell within the field of view of the sensors. P_r and P_i measurements were taken at 1 min intervals. The height and the area covered in the FOV of the P_r sensors at the various stations above the different plant canopies can be found in Tables 2.3 and 2.4.

Table 2.3 Height of PRI sensors above the canopy and area that fell within the FOV.

Species	Height above canopy (m)	Area within the FOV (m^2)
	Site 1	
A. selaga	0.13	0.084
S. procumbus	0.23	0.15
	Site 2	
A. magellanica	0.10	0.065
A. stolonifera	0.17	0.11
	Site 3	
R. lanuginosum	0.17	0.11
S. colorata	0.22	0.14

Table 2.4 Height of infrared thermometer (IRT) sensors above the canopy and area that falls within the FOV.

Species	Height above canopy (m)	Area within the FOV (m^2)
	Site 1	
A. selaga	0.165	0.05
S. procumbus	0.29	0.16
	Site 2	
A. magellanica	0.1	0.02
A. stolonifera	0.24	0.11
	Site 3	
R. lanuginosum	0.23	0.1
S. colorata	0.23	0.1

All the downward facing SRS sensors were mounted to face the same azimuth and solar zenith angles in order to minimize the sun-sensor-surface reflection effect on the spectral reflectance signal (Hilker *et al.* 2008; Gamon *et al.* 2015). All measurements were logged and stored by an Em50 data logger from Decagon Devices.

In order to calculate the reflectance, the measurements taken by the downward facing sensors (P_r) were compared to the corresponding measurements taken by the upward facing sensors (P_i) for both wavebands measured. The reflectance can therefore be measured by dividing the radiance measurements taken by the downward facing sensor by the corresponding irradiance measurements taken by the upward facing sensor:

Equation 2.3 Reflectance calculation of 531 nm waveband

$$P_{531} = \frac{P_{r531}}{P_{i531}}$$

Equation 2.4 Reflectance calculation of 570 nm waveband

$$P_{570} = \frac{P_{r570}}{P_{i570}}$$

The PRI can then be calculated by using the following equation:

Equation 2.5 PRI calculation

$$PRI = \frac{P_{531} - P_{570}}{P_{531} + P_{570}}$$

where P_{531} and P_{570} are the percentage of reflectance at the specific wavelengths of 531 and 570 nm respectfully (Gamon *et al.* 1992; Penuelas *et al.* 1995).

PRI values range between -1 and 1 with -1 usually interpreted to indicate maximum and 1 indicating optimal photosynthetic conditions. However, readings are likely to show some level of species-specific behaviour and thus ancillary measurements of leaf chlorophyll fluorescence and leaf chlorophyll content via independent intrumentation was repeated through the year, and intensively on one occasion during the growing season on multiple individuals in the vicinity of the fixed point measurements. These measurements provided general support for the PRI measurements as an indicator of physiological stress, and confirmed that the point monitoring of individual canopies was representative of surrounding vegetation.

2.3.Field chlorophyll fluorescence (optical measurements)

Chlorophyll fluorescence was measured using a PAM-2500 Chlorophyll Fluorometer, manufactured by Heinz Waltz GmbH, Germany. A modified dark leaf clip (DLC-8) was used for measuring chlorophyll fluorescence on bryophytes. For all other plants a Heinz Waltz leaf clip holder 2030-B was used. The dark leaf clip was modified by creating a hole in the bottom part of the dark leaf clip in order to expose the plant sample to the fibre optic sensor.

Fm' (maximum fluorescence of an illuminated plant) and Fo' (minimal fluorescence of an illuminated plant) was measured on all six plant species in the field. Measurements were made during the day when all plants were illuminated at the natural light intensity. The plants were afterwards dark adapted using a dark leaf clip for 20 minutes. In order to measure Fo (minimal fluorescence), the plants were exposed to a low light intensity (<1 μmol m^{-2} s^{-1}). A

pulse of a saturating light of >5000 μmol m^{-2} s^{-1} was then applied in order to measure Fm (maximum fluorescence).

Fm, Fo, Fm'and Fo' was used to calculate certain fluorescence parameters. The potential maximum quantum yield of photosystem Ⅱ (Fv/Fm) was calculated using equation 2.6 (Rohacek, 2002; Bilger *et al.* 2016).

Equation 2.6 Potential maximum quantum yield of photosystem Ⅱ

$$\frac{Fv}{Fm} = (Fm - Fo)/F$$

Fv/Fm shows the maximum efficiency or photochemistry that can take place (Rohacek, 2002; Bilger, Schreiber and Bock, 2016). It therefore shows what the maximal probability is of an absorbed photon to enter the electron transport chain. A decrease in Fv/Fm in a plant can be an indication of stress. Fv/Fm of a healthy plant is assumed to be around 0.81-0.85 (Rohacek, 2002; Bilger, Schreiber and Bock, 2016).

Non-photochemical quenching (NPQ) of fluorescence was calculated using equation 2.7 (Rohacek, 2002; Bilger *et al.* 2016).

Equation 2.7 NPQ of fluorescence

$$NPQ = (Fm' - Fm)/Fm'$$

2.4. Controlled chlorophyll fluorescence (optical measurements)

The yield of PS Ⅱ (psi PS Ⅱ) was measured of five individuals of all species studied in order to determine if different individuals of a species are atypical in their photosynthetic responses. Five live individuals of each species were collected. All individuals were collected within a 100 m radius from the original study plant.

All individuals were acclimated in a growth chamber under a stable light environment and ambient air temperature of 6°C, as is typical on Marion Island. The plants were acclimated for 30 minutes under a stable light source of 100 micromol/m/s. The yield of PS Ⅱ was measured of each individual. This was repeated three times in order to account for changes in psi PS Ⅱ due to unaccounted stress. Each individual was also weighed before and after each measurement in order to account for stress due to water loss.

2.5. Controlled spectral reflectance measurements

The downward facing spectral reflectance sensor (P_r) was used to measure reflectance of all species under controlled conditions to determine if the measurements taken by the spectral reflectance sensors are similar between different individuals of the same species.

Five live individuals of each focal species was collected. All individuals were collected within a 100 m radius from the original study individual. All individuals were acclimated in a growth chamber under a stable light environment and ambient air temperature of Marion Island (6°C). The reflectance of the each individual was measured for 10 minutes under a stable light source of 100 PAR. This was repeated three times for each individual. Each individual was weighed before and after each measurement in order to account for stress due to water loss.

An average of the reflectance measurements for each 10 minutes was used to compare the reflectance signal between individuals and species.

2.6. Chlorophyll content

The total chlorophyll content (mg m^{-2}) of all the focal species was measured with the CCM-300 Chlorophyll Content Meter (Opti-Science Inc.). The CCM-300 is a fluorometer and uses a modulated fluorescence ratio technique.

Total chlorophyll content of five leaves was taken from the following species:

- *A. magellanica*
- *A. stolonifera*

Due to the difficulty of measuring chlorophyll content of individual leaves, five measurements of surface chlorophyll was taken of the following species:

- *A. selago*
- *S. procumbus*
- *R. lanuginosum*
- *S. colorata*

Total chlorophyll content was measured of all the focal species every two weeks in order to get an accurate profile of how chlorophyll content changed during the various seasons.

2.7. Physical measurements

The soil volumetric water content (SVWC) (m3/m3) measurements was taken at each of the plant communities. Measurements were taken by a GS3 sensor manufactured by Degacon Devices . The measurements was taken at a depth of 5 cm. The soil temperature (Celsius) was also taken with the GS3 sensor at each site.

All SVWC and soil temperature measurements were measured and stored by Decagon's Em50 data loggers. Measurements were taken at 10 s intervals and were logged at 1 min intervals as an average of the 10 s measurements.

2.8. Meteorological measurements

Meteorological measurements were taken and stored by Decagon's Em50 data loggers. All meteorological measurements were taken at the same altitude as the three remote sensing stations. A sonic anemometer manufactured by Degacon Devices was used to measure wind speed and direction. The anemometer was mounted 0.5 m above the ground and was orientated north in order to get accurate data as instructed by Decagon Devices manual. Measurements were taken at 10 s intervals and were logged at 1 min intervals as an average of the 10 s measurements.

Air temperature (Celsius), barometric pressure (kPa) and relative humidity (%) were measured with the Vp4 sensor (Decagon Devices). The Vp4 sensor was mounted at 0.5 m. Measurements was taken and logged at 1 min intervals. Solar radiation (W m^{-2}), at wavelengths of 380 to 1120 nm, was taken by a pyronometer (Solar Radiation Sensor: Decagon Devices). The pyronometer was mounted 1 m above the ground with the sensor pointing to the nearest magnetic pole which was the South Pole.

2.9. Data analysis

All data analysis was done using the R programming language, using the Rstudio user interface (RStudio, 2015). Data analysis will be discussed in each chapter.

3. Marion Island and the climatic environment

3.1. Abstract

Seasonal variability in climate has been described as muted, however variability on small time scales (diurnal) has not yet been thoroughly explored and may be important in characterizing the biophysical environment of Marion Island. The aim of this chapter is therefore to explore the variability of climate on various temporal scales. High resolution measurements of one minute were taken of meteorological and biophysical variables in order to explore the variability in climate on Marion Island for the period of May 2016 to April 2017. Cyclic behaviour was seen in all variables, however this was not significant and changes in seasons could therefore not be clearly defined. Diurnal temperature ranges were high, creating high variability on small time scales. Freezing temperatures were not isolated to colder months, but could be experienced at virtually any time of the year. The passing of clouds over the island creates a highly variable light environment, where high levels of solar irradiance can be experienced in short bursts throughout the day. There was a high occurrence of low pressure systems passing this island, contributing to cloud formation on the island. Even though low pressure systems frequently passed the island, low annual precipitation levels were still measured. Increase in wind speeds during the month of November, December and January could be seen with North-westerly winds being dominant. Low humidity levels of below 20% were occasionally measured on the island, however they were not exclusively connected to Föhn winds as previously thought. Continuous monitoring of climate on Marion Island by South Africa National Weather Station (SAWS) has shown an increase in sunshine hours with decreased rainfall. Marion Island is therefore becoming warmer and drier. With these climate trends continuing, significant changes in the ecology of Marion Island can be experienced with climate shifts.

3.2. Introduction

Marion Island has a hyper-oceanic climate and is highly influenced by frontal systems passing over the island (Smith and Steenkamp, 1990). Consequently, the physical environment of Marion Island is characterized by high moisture content and the terrestrial ecosystem is classified as an important wetland according to The Convention on Wetlands of International Importance, better known as the RAMSAR Convention (Cooper, 2010). The dominant form of precipitation occurring on the island is rain, however mist and fog are common place, with snow and ice pellet precipitation also prevalent, especially in winter months of June, July and August (Schulze, 1971).

The air temperature measured on the island is closely linked to the temperature of the ocean, because the surrounding oceans act as a thermal buffer. The annual range of monthly mean temperature on the island is therefore small (±4 °C between "summer" and "winter") and a clear seasonal difference is not seen (Smith and Steenkamp, 1990; Smith, 2002). Cloud cover on the island restricts incoming solar radiation, with only ±30% of the potential incoming solar radiation reaching the surface (Schulze, 1971). This affects the terrestrial temperature on the island, and a lag in change of temperature behind the solar input can be seen. Wind speeds experienced on Marion Island are high, with average wind speeds are measured at 9 m/s (Smith and Steenkamp, 1990).

Muted seasonality has been reported on Marion Island due to the thermal buffer regime provided by the southern ocean (Smith and Steenkamp, 1990). While this has been well recognised, the variability on small time scales may be important in characterizing the biophysical environment of the island. With variability across seasons being small, it is important to understand variability in the climate on a small time scale (diurnal) to capture the nature of the environment.

Continuous monitoring of climate by the meteorological station operated by SAWS shows an increase in sunshine hours with a decrease in precipitation between the period of 1960 and 2001 (Rouault, 2005; le Roux and McGeoch, 2008b). This has led to an increase in temperature over the past few decades. The effect of climate change can be seen in the temperature shifts in the island.

This chapter will explore annual and sub-annual climate variability on Marion Island, including characteristic diurnal patterns. This will include the temperature ranges of soil and air temperatures, the light environment and changes in moisture regimes seen on the island as well as the frequency of extreme events. It will aim to determine whether seasonal differences in climate that have previously been described as muted can be characterised using this finer temporal scale approach, and whether a clearer difference in seasonal conditions for plant growth can be defined based on meteorological and biophysical measurements.

3.3. Data analysis

Summary statistics were developed for all meteorological and biophysical variables in order to determine mean, maximum and minimums at annual and monthly time scales. Time series graphs were drawn with mean monthly values and error bars for the period of March 2016 to May 2017.

For air temperature a two tailed t-test was done to determine whether there is a significant difference between night and day time temperatures for continuous 24-hour periods. A linear regression was done to determine the relationship between solar irradiance and day-time air temperature. A Pearson correlation was done between soil temperature and air temperature. Due to the size of the dataset, an Anderson Darling test was done in order to test for normality. Tests for normality, linearity and homogeneity were done on all variables.

Distribution histograms of atmospheric pressure were developed to determine the frequency of passing high and low pressure systems. Pearson correlations between relative humidity, pressure, wind speeds, and wind direction were performed. Frequency counts were performed on wind direction to determine the dominant wind direction as well as the dominant wind directions associated with atmospheric pressure conditions.

To determine if there was cyclic behaviour in all measured variables, the seasonal component of the dataset was modelled. The annual cycle was scaled to be the length of 1.0 (1.0 = 365 days). A regression was done with a sigmoidal curve ($y = \alpha + \beta\sin(2\pi t) + \gamma\cos(2\pi t) + \varepsilon$). Based on these results, a k-means clustering was done in order to determine if there is a clustering between “summer” and “winter” seasons. Daily means were used in the k-means clustering.

3.4. Results

3.4.1. Variability, extremes and trends of meteorological and physical measurements.

An overview of mean, minima and maxima measurements made for different environmental variables are given in Table 3.1.

Table 3.1 The annual mean, minimum and maximum measurements of all meteorological and biophysical measurements as measured on Marion Island form May 2016 to March 2017 (* = values are zero since a lower value cannot be measured for respective variables; ** = values not given since measurement fell outside of the range of the sensor, * = total is given instead of mean).**

Variable	Mean	Max	Min
Solar irradiance (% of maximum)	15.58	100	*
RH (%)	87	100	21
Pressure (kPa)	100.62	103.58	95.62
Air Temperature (Celsius)	6.39	26	-4.1
Wind speed (m/s)	7.95	**	*
Soil Temperature(Celsius)	6.14	23.8	-2.1
Soil water (m3/m3)	0.25365	0.319	0.009
Precipitation (mm)	1887.8***	-	-

Air Temp

Due to the thermal buffering provided by the Southern Ocean, fluctuations in annual air temperature are moderate and the mean difference between the monthly ranges are only ±4.5°C measured in 2016/2017 (Figure 3.1) and only ±4°C mean hourly difference were measured. Although the mean temperature cycle on Marion Island is muted, there is high variability between maximum and minimum temperatures measured on the island. A maximum air temperature of 26°C was measured during the month of March 2017 and a minimum temperature of -4.1°C was measured during July 2016.

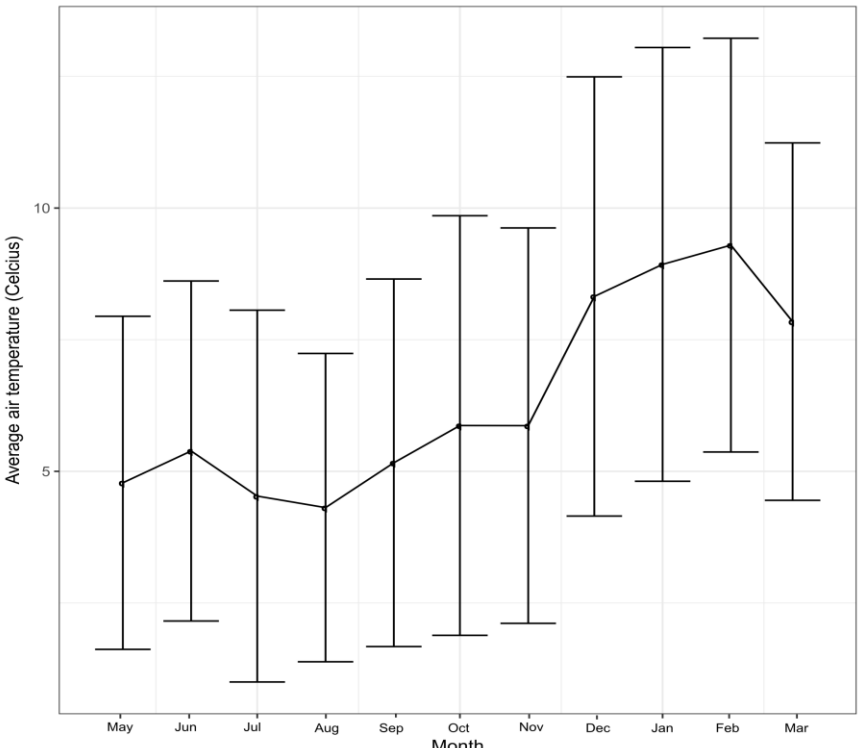

Figure 3.1 Monthly mean air temperature measured on Marion Island with standard deviation bars. Air Temperature (day and night time temperatures) was measured for the period of 2016/2017.

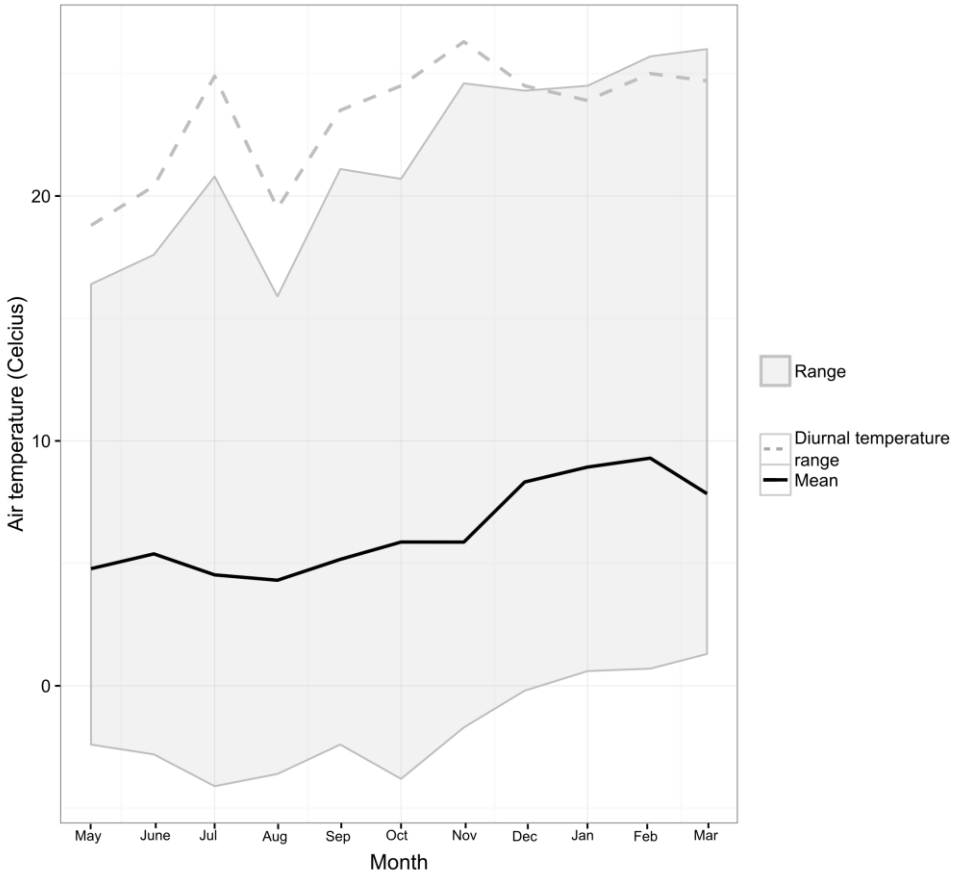

Figure 3.2 Temperature ranges throughout the season including mean temperature, maximum and minimum temperatures. Averaging of daily ranges per month used.

Diurnal temperature variability can be seen in in temperature ranges experienced throughout the day. Daily temperature ranges can be up 20°C as measured on the 31/07/2016 with a minimum air temperature of -2.7°C and a maximum air temperature of 18°C. Daily temperature ranges do not change seasonally, with daily temperature ranges being similar throughout the change of the seasons (Figure 3.2).

A discrepancy can be seen in temperature measured in this study and by the Marion Island meteorological station operated by SAWS, where a maximum temperature of 11.9°C and a minimum air temperature of 1.2°C were measured in the same year. This is to be expected since the air temperature during this study was taken at a different height compared to the air temperature measured by SAWS> Sub-zero temperatures were experienced throughout the year on various days; with the coldest temperature recorded during the "winter" months of June, July and August (Figure 3.3). A clear shift can be seen where sub-zero temperatures did not occur and daily average high temperatures were measured during January, February and March as depicted in Figure 3.3.

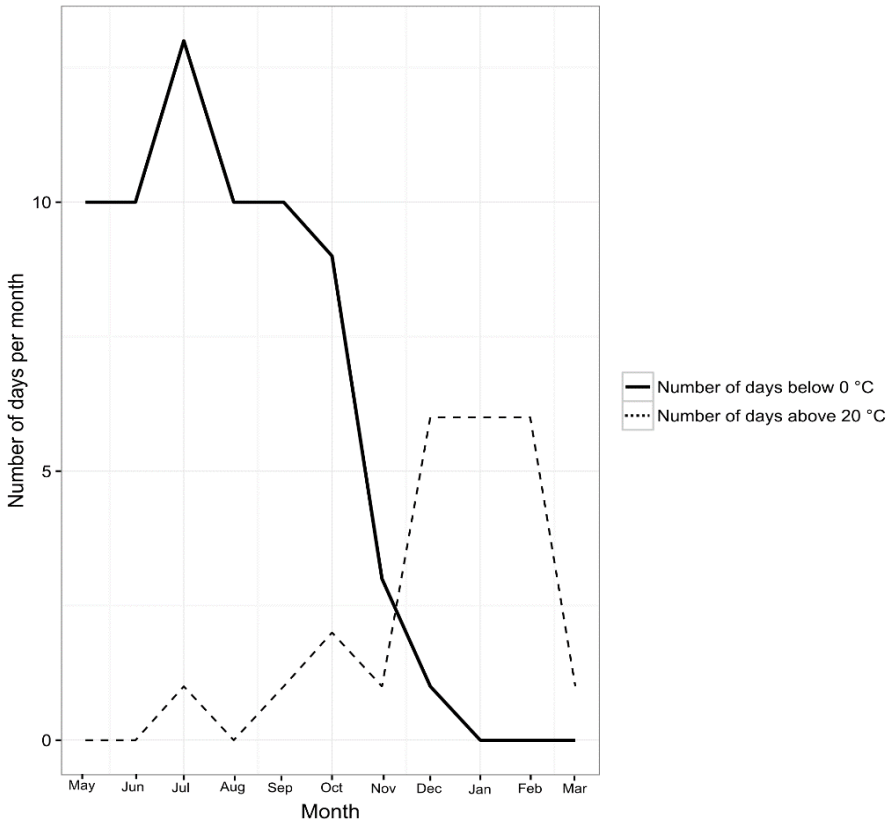

Figure 3.3 Number of days where air temperature was recorded at any point during the day below or above indicative thresholds.

The thermal inertia of the island provided by the buffer regime of the southern ocean can be seen in the lag of increase in air temperature behind the solar radiation input. A

peak of solar radiation input was seen in the month of December 2016, however maximum air temperatures were only measured in January 2017 (Figure 3.1 and Figure 3.4). The relationship between solar radiation and daily air temperature appear to be linear (slope = 0.007, $R^2 = 0.334$, $p < 0.05$). This relationship increases slightly if the variables are lagged by one month (slope = 0.007, $R^2 = 0.391$, $p < 0.05$). Average maximum temperatures are not experienced at midday, but towards 14:30.

The mean air temperature measured during the day differed significantly from the mean air temperature measured during the night (paired sample t-test: df = 544810, $p < 0.001$, t = -420.813). Mean night-time air temperatures are colder (annual mean = 6.35°C) than mean day-time temperatures measured (annual mean = 8.05°C).

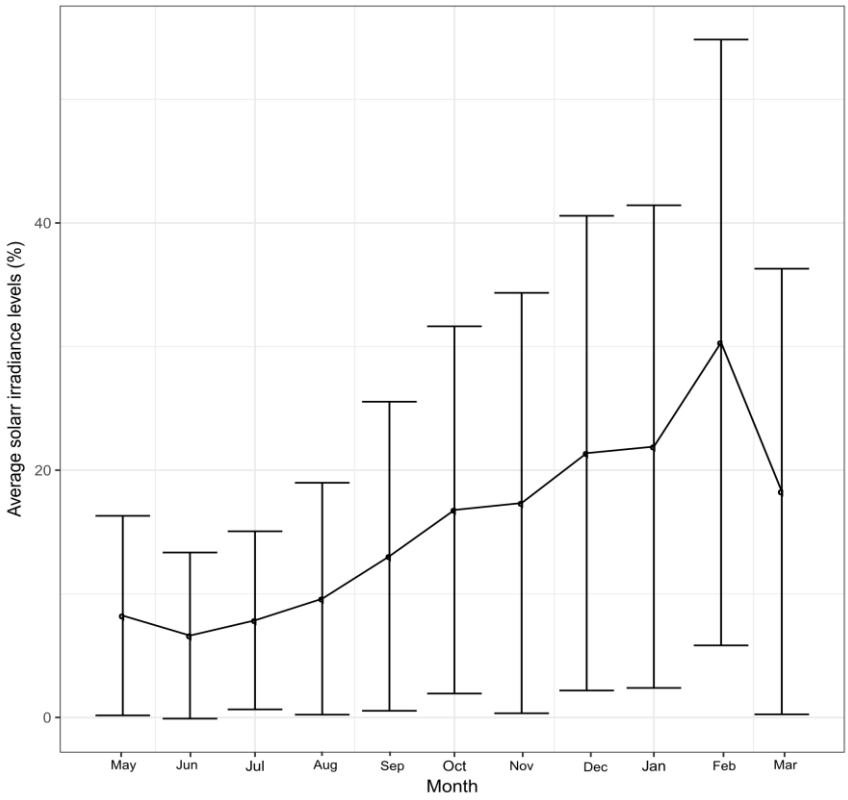

Figure 3.4 Monthly mean solar irradiance measured on Marion Island with standard deviation bars. Solar irradiance was measured for the period of 2016/2017.

Wind

In 2016/2017 there were only 13 days where wind speeds did not reach a maximum of more than 5 m/s. Northern winds were the most predominant on the island with more than 40% of observation during 2016/2017. Westerly winds were the second most predominant winds observed during 2016/2017 (±15%). Southern winds were the least dominant on the island with less than 15% of the observations during 2016/2017 (Figure 3.5).

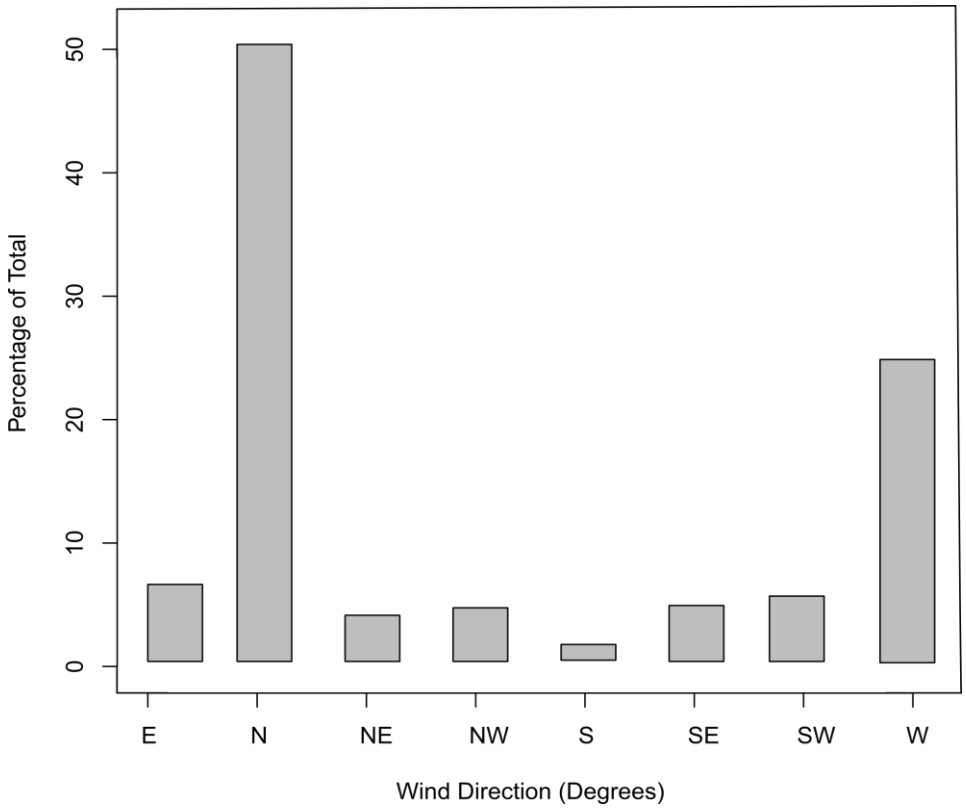

Figure 3.5 Compass distribution of wind directional observations during the period of 2016/2017 on Marion Island.

In 2016/2017 a maximum average monthly wind speed of ±19 m/s was measured in January. The maximum gust speed was above the range of the DS-2 anemometer, however this was only for short time periods on selective days. The meteorological station operated by SAWS measured a maximum gust of 55.8 m/s in June 2016.

A diurnal pattern in wind speeds can be seen with wind speeds on average being higher during the day than at night.

A strong increase in average daily wind speeds were seen during November, December and January (Figure 3.6).

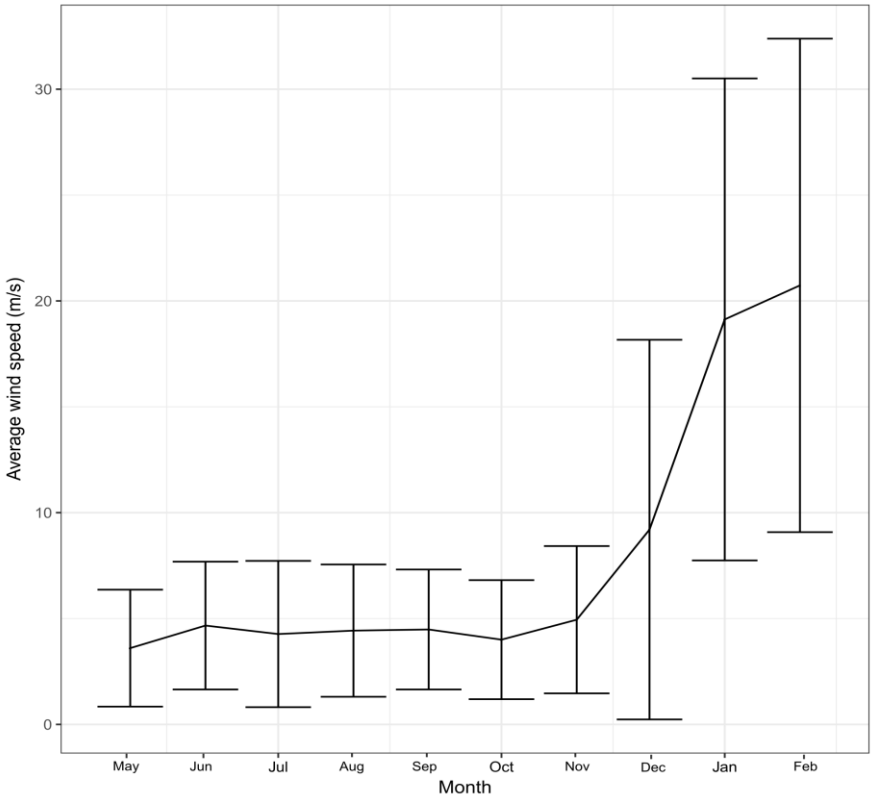

Figure 3.6 Monthly mean wind speeds measured on Marion Island with standard deviation bars. Wind speeds was measured for the period of 2016/2017.

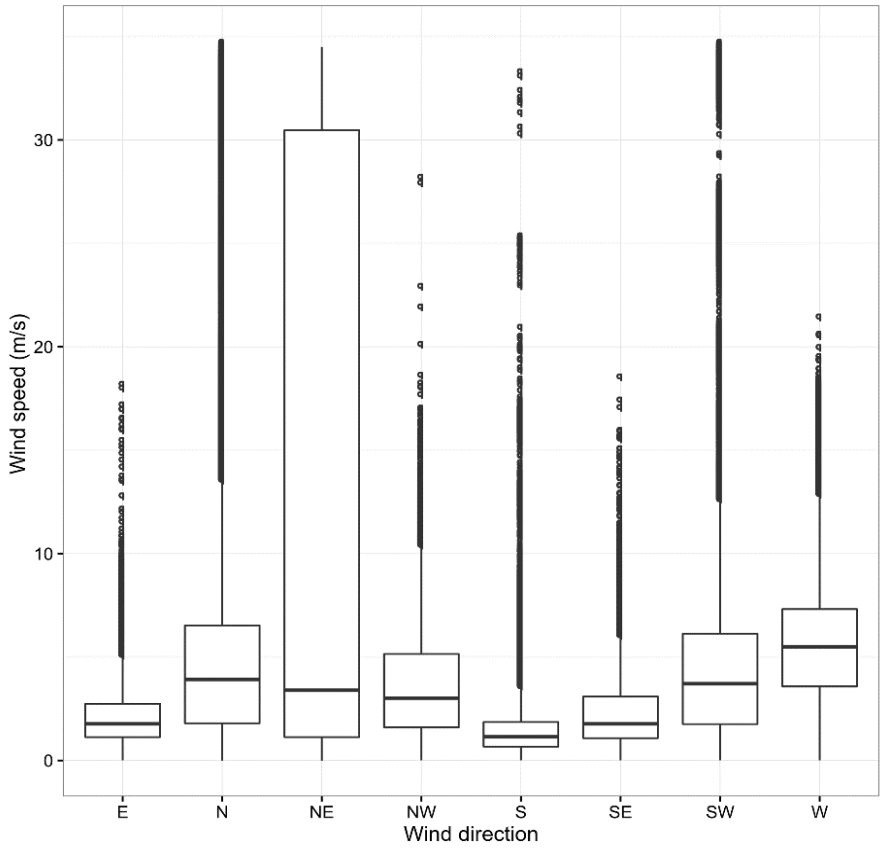

Figure 3.7 A comparison of daily average wind speeds experienced from different wind directions (single factor ANOVA: $F = 16925$, $p < 0.001$)

A single factor ANOVA revealed a significant difference in wind speeds across different wind directions ($F = 16925$, $p < 0.001$). A post-hoc Tukey test showed that wind speeds measured from different directions were significantly different from each other besides South East ~ East ($p = 0.99$) and South ~ West ($p = 0.04$) only being slightly significantly different (Figure 3.7).

Pressure

The lowest average pressure experienced on the island was during the month of December 2016 with atmospheric pressure dropping below 100 kpa (Figure 3.8). This coincides with the highest rainfall also experienced within the month of December 2016. The lowest atmospheric pressure was measured in October 2016 and the highest atmospheric pressure was measured in July 2016.

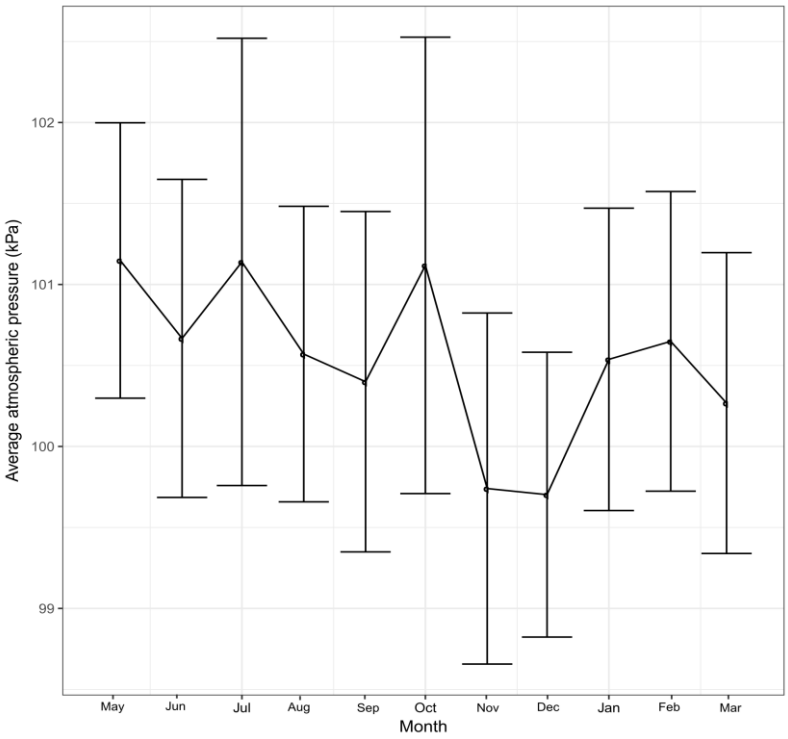

Figure 3.8 Monthly mean pressure measured on Marion Island with standard deviation bars. Pressure was measured for the period of 2016/2017.

Twenty-seven percent (27%) of the observed atmospheric pressure measured was lower than 100 kPa indicating the passing of low pressure systems. Eleven percent (11%) of the observed atmospheric pressure was higher than 102 kPa with only 2% of observed atmospheric pressure being higher than 103 kPa (indicating the passing of high pressure systems). (Figure 3.9).

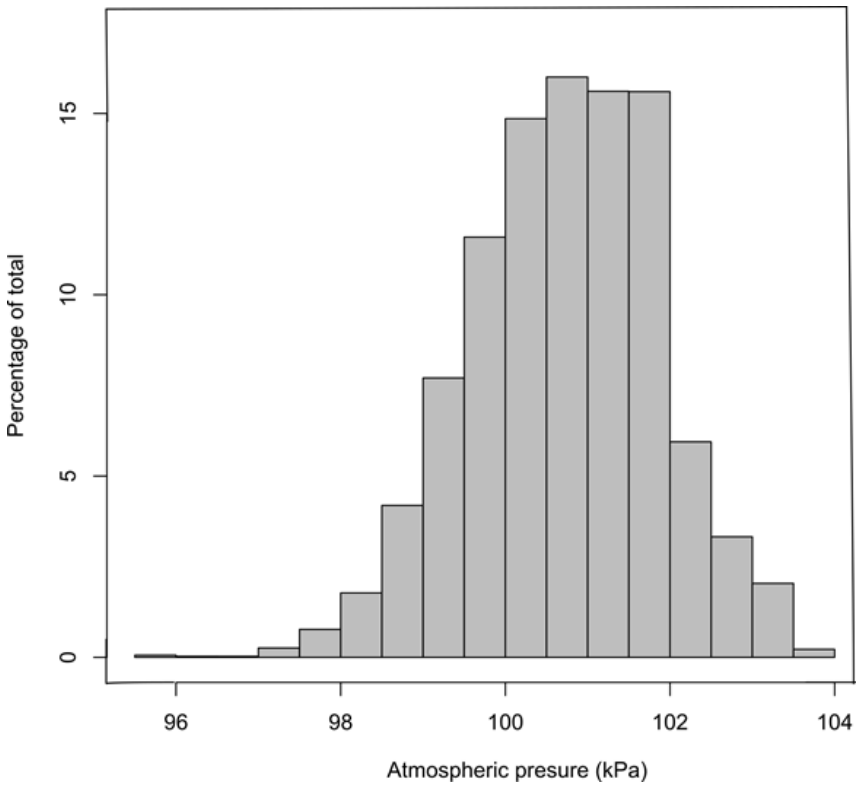

Figure 3.9 Distribution of atmospheric pressure measurements made during the period of 2016/2017 on Marion Island

Easterly winds were associated with the average highest atmospheric pressures measured (mean = 100.98 kPA) with North-westerly winds connected with the second highest average atmospheric pressure (mean = 101.97 kPa). Westerly winds and South-westerly winds were connected with the lowest average atmospheric pressure measured during 2016/2017.

Solar irradiation

The pyronometer could not be calibrated on Marion Island with solar irradiance measurements by SAWS due to technical difficulties experienced by the SAWS pyronometer, but it was calibrated in South Africa before the study commenced. Solar irradiance measurements will therefore be given as a percentage solar irradiance received out of a theoretical maximum solar irradiance, since small discrepancies might arise. The average mean solar irradiance per month measured on Marion Island ranges between 8.23% and 30.33%. This is considered low, however measurements of high incoming solar radiation levels of >60% of the maximum were observed in 10% of the measurements showing the variability of solar irradiance measured on the island (Figure 3.10). Variability of solar irradiance can be seen on a diurnal scale where solar irradiance can vary form 11% to 57% within one day. This is due to the cloud cover movement on Marion Island.

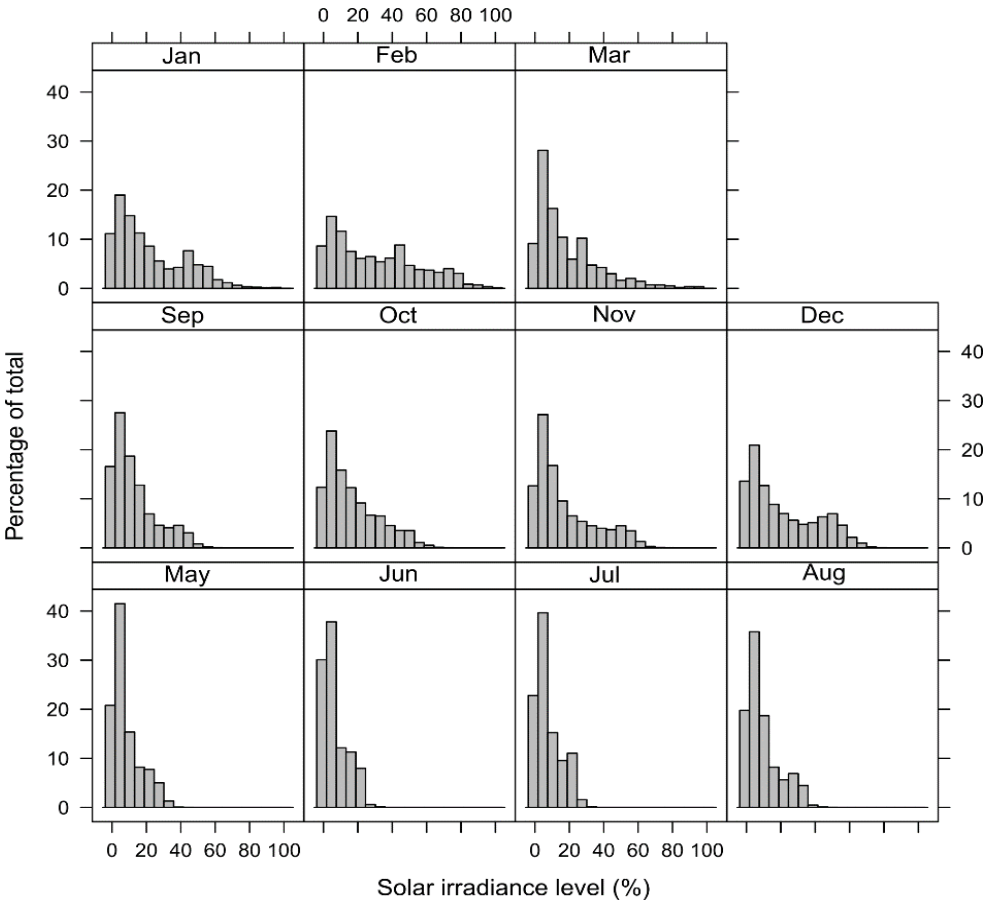

Figure 3.10 Distribution of relative solar irradiance measurements associated with different months for the period of 2016/2017 on Marion Island.

An increase of solar irradiance can be seen in February 2017 where an average level of 30.33% was experienced. This coincides with a higher distribution of observed measurements being higher than 57% in February 2017 compared to any other month (Figure 3.10). In August 2016 an average monthly solar irradiance level of 9.60% was measured. These measurements coincide with “winter” and “summer” seasons of Marion Island.

Relative humidity

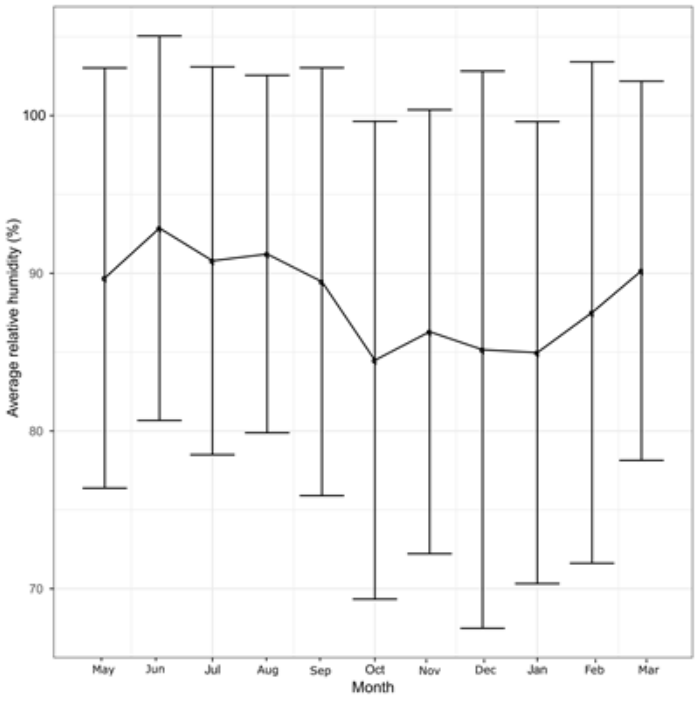

Figure 3.11 Monthly mean relative humidity measured on Marion Island with standard deviation bars. Relative humidity was measured for the period of 2016/2017.

The relative humidity on the island is high with the average relative humidity measuring between 85%-95% throughout the year (Table 3.1); however minimum relative humidity of below 30% was measured during 2016/2017. A minimum relative humidity of 21% was measured in May as well as a low relative humidity of 22% measured in December. The lowest average relative humidity was measured during October (Figure 3.11). This coincides with low precipitation experienced in October 2016.

There was a decrease in relative humidity measured during the summer months of October 2016 until January 2017 and this was on average 7% lower than the average relative humidity measured during the other months (Figure 3.11). This coincides with the warmer "summer" months seen on Marion Island.

The average highest relative humidity is associated with Westerly winds (mean = 91.8%) and the lowest average relative humidity is associated with Easterly and South Easterly winds (mean = 0.824 and 0.828 respectfully).

Precipitation

Daily mean precipitation data for the period of May 2016 until March 2017, was acquired from the meteorological station operated by SAWS based on Marion Island. The total precipitation for the period of May 2016 until March 2017 was more than 1700 mm. During the month of October 2016, the lowest total rainfall was measured (99.8 mm) while the highest monthly rainfall was measured during the month of December (320.2 mm).

Soil thermal and moisture properties

Soil temperature

The mean monthly variation in soil temperature was small (±5°C). Diurnal variability in soil temperature was much higher than this, with the highest diurnal variability measured on the 12/09/2016 of 24.3°C. This includes both soil temperatures throughout the night and day. The variability in soil temperatures measured during the night was much higher (mean temperature range = 7.54°C) than the soil temperatures measured during the day (mean temperature range = 6.35°C).

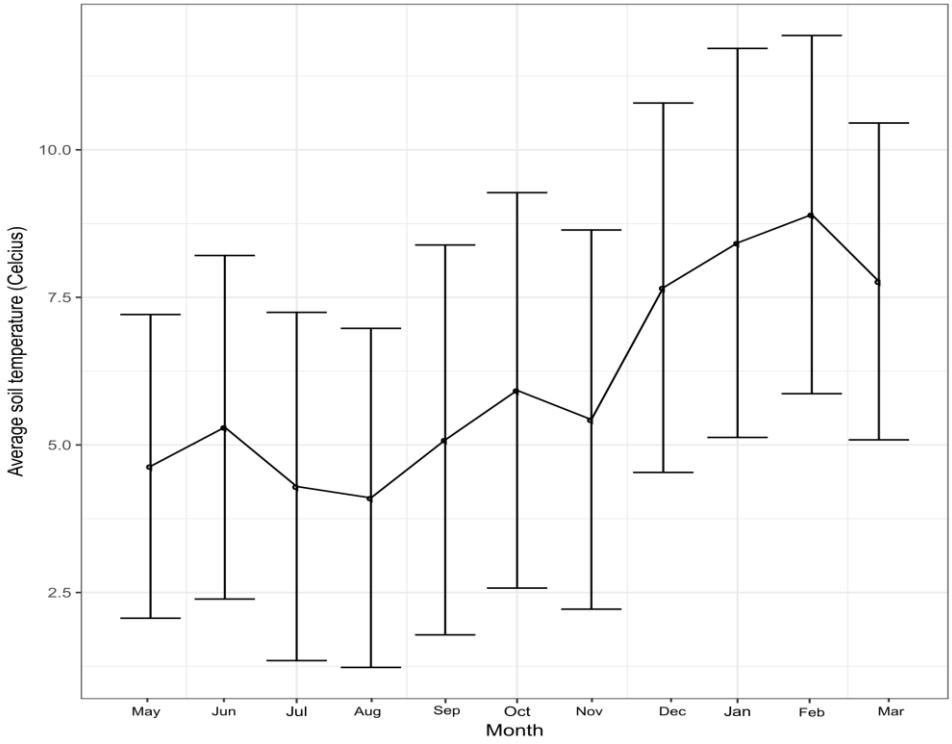

Figure 3.12 Monthly mean soil temperature measured on Marion Island. Soil temperature was measured for the period of 2016/2017.

The highest average monthly soil temperature was measured during February 2017 and the average lowest monthly temperature was measured in August 2016. The highest soil

temperature was measured in September 2016 and the coldest soil temperature was measured in July 2017 (Figure 3.12). Soil temperatures measured during the night were on average 1°C colder than soil temperatures measured during the day. The mean soil temperature measured during the day differed significantly from the mean soil temperature measured during the night (paired sample t-test: df = 544810, $p < 0.001$, t = -307.73).

There was a strong positive correlation between air temperatures and soil temperatures measured on the same day (Pearson's correlation: $r = 0.91$, $p < 0.001$).

Soil Volumetric Water Content (SVWC)

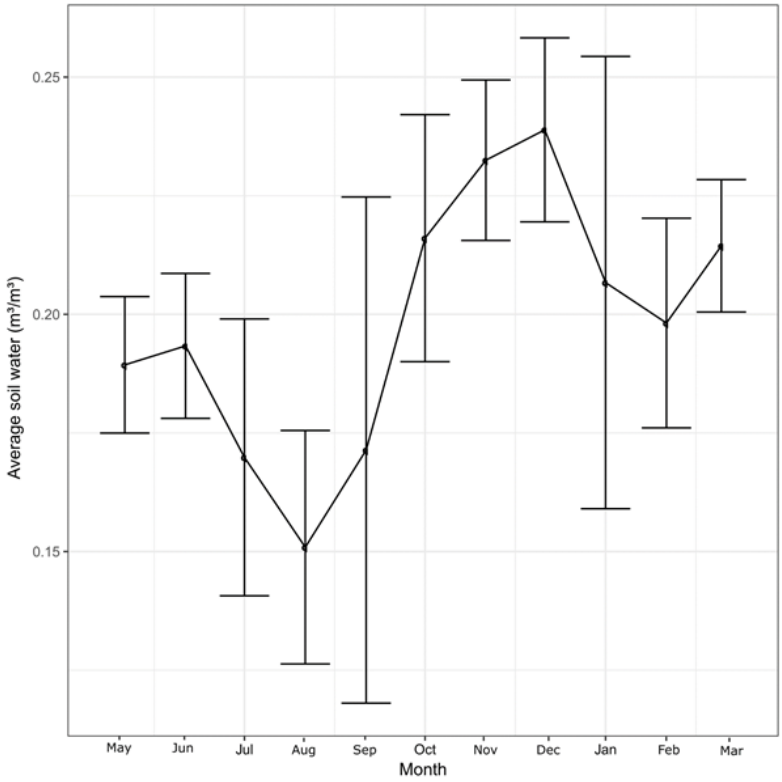

Figure 3.13 Monthly mean soil water measured on Marion Island with standard deviation bars. Soil water was measured for the period of 2016/2017.

Soil water was measured on a volumetric basis (SVWC). SVWC increased during the "summer" months on the island with the highest mean monthly soil water measured in December 2017. The lowest mean monthly SVWC was measured during August 2016 (Figure 3.13). The maximum SVWC was measured during December and the minimum SVWC measured on the island was during July. Annual average SVWC on Marion Island was high.

A Pearson correlation revealed that there is a significant positive correlation between soil water and soil temperature with an increase in soil water as soil temperature increases ($t = 11.43$, df = 545070, $p < 0.001$).

3.4.2. Seasonal patterns in meteorological and physical measurements

Seasonal cyclic behaviour is seen in all variables besides precipitation measurements with a fit of a sigmoidal curve being significant to predict the pattern seen over time for all variables (Table 3.2). Wind was not included due to problems experienced from the DS-2 sonic anemometers which caused discrepancies in data.

Table 3.2 The regression fitting a sigmoidal curve in variables to determine cyclic behaviour over time. (Formula: y= sin (time*2*pi)+cos(time*2*pi))

Variables	R^2	F	p	df
Solar irradiance	0.2499	53.64	0.001	322
RH	0.089	15.8	0.001	322
Pressure	0.084	14.82	0.001	322
Air Temperature	0.3883	102.2	0.001	322
Soil Temperature	0.3403	83.06	0.001	322
Soil water	0.3751	96.66	0.001	322
Precipitation	0.002	0.43	0.65	426

Since there was cyclic behaviour seen in meteorological and biophysical measurements a k-means clustering was done in order to determine whether a significant change in seasons can be seen. Daily precipitation measurements were excluded from the clustering since cyclic behaviour was not seen. Daily mean and maximum temperatures for both soil and air temperatures were included as well as means of all variables to determine seasonal clustering. Days were clustered into two groupings based on meteorological and biophysical measured variables.

3.5. Discussion

Marion Island's climate has been termed as hyper oceanic (Smith and Steenkamp, 1990). The island experiences a thermal buffer regime due to the surrounding southern ocean (Schulze, 1971). This can be seen in the low ranges of mean monthly temperature measured on the island. There was cyclic behaviour seen in air temperature with an increase in the monthly mean temperature in "summer" months (November, December, January), however this is not significant. Thermal variability between months is small and can be accredited to the thermal buffering regime of the ocean surrounding the island (Smith and Steenkamp, 1990). The sea surface temperature of the surrounding ocean and the air temperature measured on Marion Island are linked, with air temperature being similar to sea surface temperature measured (Smith and Steenkamp, 1990).

Even though low temperature ranges can be seen between months, high daily variability in air temperature was still measured with large daily temperature ranges. Although high temperatures (>20º C) were measured during the study period, these temperatures were measured only for a few minutes during specific days. Temperature ranges are therefore high when looking at smaller time scales and creates a high variability in temperature throughout the day. This variability creates a temperature environment that is not as "stable" as expected due to the thermal buffer regime of the surrounding water. Due to the thermal buffer regime mean monthly temperatures are low and temperatures below freezing point (<0°C) can be measured during any time of the year.

The high temperatures measured may also be a result of the fact that temperatures were measured only 30 cm above the ground where heat radiated from the ground and canopy influences the air temperature measured. The measured air temperatures are therefore the air temperature experienced by the low lying plants found on Marion Island.

The impact of the thermal buffer regime of the ocean can also be seen in the lag between the solar energy input and changes in temperature. The highest daily temperature are measured not at midday, but later. There is a discrepancy between the months that had the highest mean temperature with the month with the highest mean solar input (Schulze, 1971). There was a significant difference between the air temperature measured at night compared to air temperature measured during the day, however the mean annual difference was small (only 2°C). This can be attributed to the thermal buffer regime of the surrounding ocean, controlling the decrease in temperature during the night when there is no solar input. Heat can also be radiating from the soil increasing air temperatures close to the ground during the night.

Marion Island's climate is highly influenced by passing frontal systems (Schulze, 1971). This can be seen on a diurnal scale as well; where the effect of cloud movement over the island can be seen in the mean maximum temperatures recorder after midday, with maximum air temperature being recorded at different times on different days.

Marion Island lies in the mean storm track and therefore has a high frequency of frontal systems passing over it (Kushner *et al.* 2000). A drop in pressure is a result of frontal systems passing over the island. The observation point on Marion island situated at sea-level and air pressure at the lower altitudes is expected to be higher than 100 kPa.

Increase in cloud cover is associated with low pressure systems. This is due to the upward clockwise movement of air within the systems. As the air moves higher in altitude, the air cools down and gets saturated promoting cloud formation (Smith and Steenkamp, 1990;

Smith 2002). The majority pressure systems passing the island for 2016/2017 were low pressure systems. During the measurement period there was almost 30% of the pressure measured dropping below 100 kPa, indicating low pressure systems moving over the island. The high frequency of low pressure systems influencing the island, correlates with the low incoming radiation levels measured due to increase cloud cover. Even though low pressure systems were measured on the island, low precipitation was still measured with annual precipitation being less than the expected 2000 mm per year.

Marion Island is characterized by high precipitation rates, which can be in the form of rain, snow, mist or ice pellets (Bergstrom and Chown, 1999). Rain is the dominant form of precipitation at lower altitudes, with rainfall being evenly distributed throughout the year (le Roux and McGeoch, 2008b). However, two periods of decreased precipitation was seen during the year between October and November and again in January 2017. This coincides with previous observations made by le Roux and McGeoch (2008). A decrease in precipitation in these months coincides with increases in solar radiation, indicating a decrease in cloud cover.

An increase in Northerly winds can be seen with a pre-cyclone period of warm weather (Smith, 2002). During December more than 40% of the observed winds were North-westerly winds. This coincides with a drastic increase in average temperature during that month as well. High pressure systems pass over the island with air circulating in an anti-clockwise manner. High pressure systems pass north of the island moving east (Smith and Steenkamp, 1990; Smith, 2002). These systems are associated with clear and dry weather. This is due to the air within the systems circulating downward becoming drier as it increases in temperature (Smith and Steenkamp, 1990; Smith, 2002). The lowest average pressure experienced on the island was during the month of December 2016 with atmospheric pressure dropping below 100 kpa.

Marion Island is situated in the “roaring forties”, aptly named for the 40° longitude of the southern ocean. Gale force winds (>15 m/s) are often experienced on the island. Gale force winds are experienced on the island on more than 100 days every year (Schulze, 1971). North-westerly winds were the dominant wind direction on the island. These winds are associated with higher temperatures and high moisture content. North-westerly winds are the strongest winds, often exceeding 10 m/s, thus contributing to the high wind speeds measured on the island (Schulze, 1971).

North-easterly winds are becoming more dominant on the island as a result of a change in the frontal systems passing over the island. This is a product of change in climate that can be seen on the island. With the winds on the island being highly influenced by atmospheric circulation patterns around the island, an understanding of the circulation patterns are needed in order to fully understand the variation in weather patterns on the island (Rouault, 2005).

High relative humidity is experienced throughout the year with annual relative humidity levels being above 80%. Low humidity is however measured on the island, sometimes dropping below 20%. Low humidity measurements have been hypothesized as being the result of Föhn winds and are only experienced for short periods of time (<5 hours at a time) (Schulze, 1971). Föhn winds are due to air that moves up over the interior on the windward side (west) of the island and loses moisture. This is due to the fact that the air cools down and the moisture holding capacity of the air declines (Smith and Steenkamp, 1990). The air then descends on the leeward (east) side of the islands. Winds and air experienced on the leeward side of the island are therefore often warmer and drier than on the windward side of the island (Schulze, 1971).

The average relative humidity measured for the period of 2016/2017 was linked to Easterly and South-easterly winds. The lowest humidity was therefore not associated with Föhn winds, indicating that the role that Föhn winds have on the island as not being as significant as previously thought.

High levels of cloud cover are experienced throughout the year and decreases solar radiation measured on the island with only 20-30% of the possible solar radiation reaching the surface (Schulze, 1971). The true effect of cloud cover can be seen on a diurnal time scale with incoming solar radiation levels ranging from 11% to more than 60% of the maximum within short time periods (less than 30 minutes). This creates a highly variable light environment throughout the day with sudden high inputs of solar radiation. The annual low solar radiation measured on the island as well as the daily cloud cover movement highlights the importance of passing frontal systems and cloud formation in defining the climate experienced on Marion Island.

Soil temperatures measured on the island were significantly higher than air temperatures measured. This can be a result of radiation received from solar inputs as well as convection of temperature from the air. Soil temperatures are influenced by a combination of air temperature, radiation balances and cloud cover (Nel *et al.* 2009). Increased soil temperatures can be due to biotic influences such as microbial activity and decomposition increasing

temperatures in soils. Plant cover also creates insulation helping to prevent the reduction of soil temperature. High variability in soil temperature are still however seen, however this coincides with the variability in solar inputs as well as variability in air temperatures. Soil temperature was measured in the top 5 cm of the soil. The temperature in the soil is therefore highly influenced by air temperature and solar radiation (Nel *et al.* 2009).

An increase in soil water can be seen with an increase in soil temperature. This can be a result of frozen water becoming available with increased temperatures. The high levels of soil water seen on the island are an effect of the high precipitation levels measured on the island. The highest mean monthly soil water content measured on the island therefore coincides with the highest mean monthly precipitation levels measured during the month of December. Moisture input form mist also contributes to high moisture levels at low altitudes.

A clear change in climate between seasons cannot be seen on the island. Cyclic behaviour however can be seen in all climate variables indicating that there is a change between the "winter" months and "summer" months, however it is not significant. This has been proposed to be due to the thermal buffer regime experienced on the island (Schulze, 1971). The lack of clear seasonality experienced in sub-Antarctic environments is one of the main characteristics that distinguishes these environments from their sub-Arctic counterparts (French and Smith, 1985). Although clear seasonality cannot be seen, shifts in climate can be seen between "winter" and "summer". These shifts include the number of days with average sub-zero temperatures and days with average temperatures of more than 20°. Change in wind speeds can also be seen, with increase wind speeds during "summer".

3.6. Conclusions

High variability in climate was measured when the climatic environment was characterized on weekly, diurnal and sub-diurnal temporal scales. This observed high variability challenges the current understanding of the Island's climate being muted due to the thermal buffering regime. Although seasons could not be definitively classified, seasonal shifts in climate can be seen between the "winter" and "summer" months.

Marion Island has experienced significant changes in climate over the past century (Bergstrom and Chown, 1999). Temperature increases are experienced at higher rates than the warming global rate, having a significant effect on the environment (Smith and Steenkamp, 1990; Bergstrom and Chown, 1999). The ice cap on Marion Island has had a significant reduction and the presence of a permanent snow line has disappeared (Sumner *et al.* 2004). These changes have not just had a significant effect on the physical environment, but also on

the biotic component of the island. Changes in vegetation structure and distribution can be seen as well changes in productivity (Chown and Smith, 1993; le Roux and McGeoch, 2008a). With these climate trends continuing, significant changes in the ecology of Marion Island are likely to be experienced with climate shifts.

4. Using PRI to track physiological changes in different functional groups on Marion Island: Description and validation of technique

4.1. Abstract

The use of remote sensing to track changes in plant physiology creates an opportunity to determine plant stress, production and physiological response over different temporal and spatial scales. PRI measures the changes in light wave bands due to the change in the carotenoid ratio of the xanthophyll cycle. PRI has been shown to correlate with other measure of photosynthetic capacity (such as NPQ and Fv/Fm), however caution needs to be applied when PRI measurements are taken in the field and interpreted. Remote sensing measurements are therefore often supplemented with field and laboratory fluorescence measurements to avoid misinterpretation. During this study both measurements of laboratory and field fluorescence were taken for this reason. The spectral reflectance signal was measured under stable conditions in the laboratory, to better interpret the PRI signal between different plant functional types. The PRI signal can be highly influenced by canopy structure and light scattering within the canopy. Caution was therefore applied to ensure that all SRS sensors were deployed at the same solar viewing angle to avoid light interference. This remote sensing effort is first of its kind on Marion Island.

The aim of this chapter is to describe the novel method of in-field PRI measurements taken on Marion Island and to validate the method. PRI measurements during this study correlated with other measures of photosynthetic efficiency and stress (Fv/Fm), indicating that field measurements of PRI may be a valuable and effective measurement tool to track plant physiology *in situ*. The variability in photosynthetic yield and the spectral reflectance signal of different individuals of the same species in the surrounding area of the continuous point samples was minimal. This indicated that measurements of single sites can be a useful indicator of the surrounding individuals. This is important, since the deployment of single stations are often used due to the cost of this technique. PRI has been shown to be a valuable indicator of plant stress and changes in plant physiology. Using high resolution measurements of PRI over multiple seasons can give new insight into the physiological changes of plant functional types on a seasonal scale as well as on a diurnal scale during different changes in season.

4.2. Introduction

Remote sensing creates the possibility to measure plant production and physiology response over different spatial and time scales non-invasively, resulting in the increasing use of optical sensors in the field (Malenovský *et al.* 2009; Harris *et al.* 2014). Temporally continuous data retrieved from remote sensing at different spatial scales can become an important supplementary measurement in conjunction with other production prediction models to determine production rates over time (Reichstein *et al.* 2007). Vegetation indexes that can be measured based on reflected wavebands (like PRI) are of particular interest since they have the potential to observe physiological changes within the plant (Malenovský *et al.* 2009; Penuelas *et al.* 2011; Harris *et al.* 2014).

PRI is based on changes within the reflected wavebands of 570 and 531 nm to track changes within the xanthophyll cycle (Gamon, *et al.* 1992; Gamon, *et al.* 1997). PRI does not directly reflect photosynthesis, but rather the necessary function of dissipating light energy that exceeds the capacity of photosystem II. The xanthophyll cycle helps to dissipate excessive light energy to prevent damage to the photosystems (Gamon *et al.* 1997). The epoxidation of violaxanthin to zeaxanthin acts as a thermal sink for excitation energy that exceeds the capacity of photosystem Ⅱ and is linked to the efficiency of photosystem Ⅱ (Penuealas *et al.* 1995; Demmig-Adams and Adams, 1996; Gamon *et al.* 1997).

Close range remote sensing can be used to track changes in chlorophyll pigments in order to measure plant production and photosynthesis on the ground. By measuring changes in xanthophyll pigment ratios, plant stress and in effect plant production can be measured in small areas (Gamon *et al.* 1992; Garbulsky *et al.* 2001). PRI has been shown to correlate with NPQ and Fv/Fm; indicating that PRI can be used to asses photosynthetic capacity (Filella *et al.* 1996; Stylinski *et al*. 2002).

PRI value ranges have been shown to be highly variable between different studies and species, making it difficult to compare results from different studies (Gamon *et al.* 1992; Penuelas *et al.* 1995; Gamon *et al.* 1997). Despite the discrepancies between different studies, PRI values have been linked to similar changes in the xanthophyll cycle (Gamon *et al.* 1992), and thus likely reflect plant functional type differences in energy dissipation processes and timing.

There have also been discrepancies between model estimations based on remote sensing techniques and ground based measurements (Harris *et al.* 2014). Canopy level measurements of PRI often do not capture the true nature of photosynthesis, since PRI measurements are

highly influenced by canopy structure and specific leaf-angle light distributions. Coupling remote sensing techniques with field and laboratory measurements of plant reflectance as well as fluorescence parameters can help to minimize discrepancies (Malenovský *et al.* 2009)..

PRI has been shown to correlate with Fv/Fm and Fv/Fm' measurements, which are used as an indicator of stress or the light use efficiency of photosystem Ⅱ (Gamon *et al.* 1992). Penuelas *et al.* (1995) showed that there is a relationship between canopy PRI measurements and fluorescence measurements of single leaves across various species, however the strength of this relationship can differ between species when fluorescence measurements are made of leaves at different levels of the canopy (Penuelas *et al.* 1995).

Another pitfall that is often associated with remote sensing techniques is the sampling of single sites. This is due to the high cost of this technique, and can lead to discrepancies when general assumptions are made about the larger area. To decrease discrepancies and avoid potential pitfalls, all PRI measurements in this study were supplemented with field and laboratory fluorescence measurements throughout the study period.

Given that this effort is the first of its kind on Marion Island, and indeed in the sub-Antarctic, the design followed is such as to maximise the range of plant functional types observed, while also building in some level of replication within functional types. The relevant logistical constraints were that only three remote sensing units were available (due to cost of the equipment) and thus an approach of following diurnal and seasonal responsiveness to environmental drivers was adopted, at fine temporal resolution, on diverse functional types. The functional types chosen are distinct, in order to increase the likelihood of discovering distinct diurnal and seasonal patterns that can be ascribed to different environmental drivers, and thus providing insight into the drivers of productivity of different communities. The aim of this chapter is to describe the novel method of in-field PRI measurements taken on Marion Island and to determine whether PRI measurements made are a reflection of physiological and environmental stress. This chapter will also focus on validating the novel method and determine whether measurements of single sites are a reflection of the surrounding species community.

4.3. Description of experimental design

Sites were chosen to maximise the diversity of plant functional groups measured as well as replicating measurements within functional groups. Only three remote sensing stations were available and focus was therefore given to gather temporal continues measurements throughout the season in order to discover diurnal and seasonal patterns.

Three distinct plant functional species provided an initial focus in order to increase the likelihood of measuring distinct physiological patterns. Within each plant functional group two focal species were chosen. Species were selected to represent not only different growth forms between functional groups, but also include diversity response of both invasive and non-invasive species. The three plant functional groups with their selected species were as follows:

1. Cushion plants
    - *Azorella selago*
    - *Sagina procumbus* (invasive species)
2. Grasses
    - *Agrostis magellanica*
    - *Agrostis stolonifera* (invasive species)
3. Lower plant species
    - *Racometirum lanuginosum*
    - *Syzigiella colorata*

Three sites where selected where two species within each functional group was represented. The remote sensing stations were designed in such a way that sensors could be rotated (by means of a rotating arm) to focus on a different species. Sensors were rotated to focus on a different species at each station every two weeks. This was to ensure that continuous data could be recorded within each month for each of the focus species to determine not only diurnal patterns, but also seasonal patterns.

Each remote sensing station included both upward facing hemispherical and downward facing spectral reflectance sensors (SRS) (Degacon Devices). Infrared thermometers were deployed in conjunction with the spectral reflectance sensors at each site. To ensure that only the canopy of the selected species fell within the field of view of the sensors, all sensors were deployed close to the canopy.

Every two weeks, seedlings of other species that might have come up and fell within the FOV of the sensor were removed. This ensured that a monoculture of only one species fell within the FOV of the sensors and to ensure that the signal received was only from the focal species.

Caution was taken to ensure that all sensors were deployed at the same viewing angles across all species and stations. In cases where doubt arose about the quality of the signal received (either due to snow coverage or movement of sensors due to strong winds) data was removed

from the data sets prior to analysis. This was specifically the case where data was removed from measurements made for *S. procumbus* since the remote sensing station was pushed over either by strong winds or interference from animals. A week of data was thus removed for *S. procumbus* in October since the exact timing of system interference could not be determined for that specific week before station setup was corrected again.

With continuous data collected, emphasis is put on trends and patterns found within the measurements in response to environmental changes. To test for commonality in response of individuals of the same species, fluorescence measurements of multiple individuals of the same species were conducted in the laboratory. The PRI reflects energy dissipated that exceeds the capacity of photosystem Ⅱ (Demmig-Adams and Adams, 1996). The yield of photosystem Ⅱ was measured of different individuals of the same species under stable conditions. Individuals were collected in a close proximity to the original study individual to ensure that all individuals were adapted to similar growing conditions. Individuals were acclimated under stable conditions in the laboratory before measurements were taken, to ensure that all plants are experiencing the same stress environment and that the measurements are therefore not a reflection of unaccounted environmental stress experienced. To account for stress due to water loss during measurements, all plants were weighed before and after each measurement.

During laboratory fluorescence measurements, the spectral reflectance signal was measured for different individuals of the same species. This was done for 10 minute increments for every individual and was repeated five times. The sensors were deployed at a fixed height and plants were placed on a white background during measurements.

4.4.Data analysis

Data used to determine the relationship between PRI, plant stress and NPQ were not normally distributed despite transformations used. A Spearman Rank correlation was therefore used to determine if there was any correlation between PRI, Fv/Fm, Fv/Fm' and NPQ measurements made. This was done on all measurements overall as well as between species and functional groups.

A Generalized Linear Model (GLM) was used to compare the photosynthetic yield of photosystem Ⅱ (psi PS Ⅱ) of the different functional groups. The data were not normally distributed so the GLM was done using a Poison distribution. The fixed effects of the model were functional groups and species. The continuous variable used for the model was the weight difference (water loss) of each sample during sampling period.

A Kruskal-Wallis Analysis of Variance was used, together with post-hoc Tukey test, to compare the psi PS Ⅱ of the different functional groups as well as for different species.

To determine if there was an intra-specific difference between psi PS Ⅱ of the different species, a GLM with Poisson distribution was used. The fixed effect and continuous variables used in this model were individuals (per species) and the weight difference (water loss) of each sample.

Similar GLM models with Poison distribution was used to determine if there was inter- and intra-specific differences for the spectral reflectance measurements for all the species used during the study. The same fixed effects and continuous variables was used as before mentioned. To account for the negative values measured with the spectral reflectance sensor (range -1 to 1), the spectral reflectance measurements were square root transformed.

4.5. Results of the validation procedures

4.5.1. PRI as a proxy for plant stress and non-photochemical quenching (NPQ)

There was overall a strong positive correlation between Fv/Fm measurements and PRI measurements (Spearman rank correlation: $r_s = 0.619$ $p < 0.05$) as well as between PRI and Fv/Fm' (Spearman rank correlation: $r_s = 0.561$ $p < 0.05$). There was a significantly negative correlation found between Fv/Fm' measurements and NPQ values calculated from fluorescence measurements (Spearman rank correlation: $r_s = -0.272$, $p < 0.05$). There was no correlation between PRI values and NPQ values measured (Table 4.1).

Table 4.1 Spearman rank correlations between overall (all species) Fv/Fm', Fv/Fm, NPQ and PRI. Values representing r values (* p < 0.05, ** p <0 .01, ***p<0.001).

	Fv/Fm'	**Fv/Fm**	**PRI**	**NPQ**
Fv/Fm'	-	**0.791***	**0.561***	**-2.72***
Fv/Fm	**0.791***	-	**0.619***	0.002
PRI	**0.561***	**0.619***	-	-0.083
NPQ	**-0.272***	0.002	-0.083	-

There was a significant positive correlation between Fv/Fm and PRI measurements for the graminoid functional group (Spearman rank correlation: $r_s = 0.337$, $p < 0.05$). There was a significant negative correlation between Fv/Fm and NPQ measurements as well as between Fm/Fm' and PRI for with in the graminoid functional group (Spearman rank correlation: rs = -0.239, $p < 0.05$; rs = -0.508, $p < 0.05$) (Table 4.2). There was a significant negative correlation between Fv/Fm' and NPQ measurements for measurements made within the cushion plant functional group (Spearman rank correlation: rs = -0.258, $p < 0.05$). There was no correlation between PRI and Fv/Fm measurements made for the cushion plants (Table 4.2).

Table 4.2 Spearman rank correlations between Fv/Fm', Fv/Fm, NPQ and PRI within the different functional groups respectfully. Values representing r values (* p < 0.05, ** p < 0 .01, ***p < 0.001).

Cushion Plants				
	Fv/Fm'	**Fv/Fm**	**PRI**	**NPQ**
Fv/Fm'	-	-	-	-
Fv/Fm	**0.621***	-	-	-
PRI	-0.076	-0.076	-	-
NPQ	**-0.258***	0.183	-0.129	-
Graminoids				
	Fv/Fm'	**Fv/Fm**	**PRI**	**NPQ**
Fv/Fm'	-	-	-	-
Fv/Fm	**0.741***	-	-	-
PRI	**0.201***	**0.337***	-	-
NPQ	**-0.508***	**-0.239***	0.014	-
Lower Plants				
	Fv/Fm'	**Fv/Fm**	**PRI**	**NPQ**
Fv/Fm'	-	-	-	-
Fv/Fm	**0.647***	-	-	-
PRI	**0.439***	0.180	-	-
NPQ	-	-	-	-

There was a significant positive correlation between Fv/Fm measurements and PRI measurements for the lower plant species (Spearman rank correlation: $r_s = 0.469$, $p < 0.05$). Due to problems experienced with field fluorescence measurements for the lower plant species, both light and dark adapted Fo/Fo' and Fm/Fm' could not always be obtained during

the same sampling period and therefore NPQ could not be reliably calculated for the lower plant species (Table 4.2).

4.5.2. Testing for commonality in the response of individuals of the same species

There was a significant difference in the psi PS Ⅱ of the different functional groups (W = 6.901, p <0.05). Looking at the individual species there was a significant difference between the psi PS Ⅱ of the different species (W= 50.006, p < 0.05). The post-hoc test showed that the photosynthetic yields of the grasses (*A. stolonifera* and *A. magellanica*) were not significantly different as well as the photosynthetic yield of *R. lanuginosum* and *S. procumbus* (Table 4.3).

Table 4.3 Multiple comparisons z-values of the psi PS Ⅱ for different species. (Kruskul-Wallis test: H = 353.5249, p < 0.001). The values represent z-values (* p < 0.05, ** p < 0 .01, ***p < 0.001).

	A. selago	*S. procumbus*	*A. magellanica*	*A. stolonifera*	*R. lanuginosum*	*S. colerata*
A. selago	-	-	-	-	-	-
S. procumbus	**6.013*** **	-	-	-	-	-
A. magellanica	**13.304*** **	**7.291*** **	-	-	-	-
A. stolonifera	**15.499*** **	**9.486*** **	2.195	-	-	-
R. lanuginosum	**4.350*** **	1.663	**8.953*** **	**11.149*** **	-	-
S. colerata	**11.508*** **	**5.495*** **	1.796	**3.990*** **	**7.158*** **	-

There was no significant difference in the psi PS Ⅱ measured between different individuals of the same species (Table 4.4).

Table 4.4 Results of GLM with Poison distribution of psi PS Ⅱ of different individuals within the same species.

	Waltz-statistic	**p-values**
A. selago	0.017	>0.05
S. procumbus	0.142	>0.05
A. magellanica	0.156	>0.05
A. stolonifera	0.155	>0.05
R. lanuginosum	0.024	>0.05
S. colerata	0.046	>0.05

There was a significant difference between the spectral reflectance measurements made between the different species (W = 13.105, p < 0.05). The post-hoc test revealed that there was a significant difference in the spectral reflectance signal between most of the species, but not between all of them (Table 4.5). There was no significant difference between the spectral reflectance signal measured between the different functional groups (W = 0.903, p > 0.05).

Table 4.5 Multiple comparisons z-values of the spectral reflectance signal for different species. (Kruskul-Wallis test: H = 13.105, p <0.05). The values represent z-values (* p < 0.05, ** p <0 .01, ***p<0.001).

	A. selago	*S. procumbus*	*A. magellanica*	*A. stolonifera*	*R. lanuginosum*	*S. colerata*
A. selago	-	**6.693*** **	0.408	**9.519*** **	**5.045*** **	**6.698*** **
S. procumbus	**6.693*** **	-	**6.285*** **	2.827	1.648	0.005
A. magellanica	0.408	**6.285*** **	-	**9.112*** **	**4.637*** **	0.413
A. stolonifera	**9.519*** **	2.827	**9.112*** **	-	**4.475*** **	2.827
R. lanuginosum	**5.045*** **	1.648	**4.637*** **	**4.475*** **	-	**5.049*** **
S. colerata	0.005	**6.698*** **	0.413	**9.524*** **	**5.049*** **	-

There was no significant difference between the spectral reflectance signals measured between different individuals of the same species (Table 4.6).

Table 4.6 Results of GLM with Poison distribution of spectral reflectance signal measured between different individuals within of the same species.

	Waltz-statistic	**p-values**
A. selago	1.018	>0.05
S. procumbus	2.302	>0.05
A. magellanica	3.579	>0.05
A. stolonifera	0.189	>0.05
R. lanuginosum	1.720	>0.05
S. colerata	1.280	>0.05

4.6. Discussion

Signal interference in PRI measurements are often experienced and caution needs to be taken to reduce interference. PRI signals can be affected by canopy structure, changes in pigments not relating to the xanthophyll cycle, “background effects” (such as soil colour, shadows) or variation in viewing and illumination angles (Barton and North, 2001; Garbulsky *et al.* 2011).

During this study caution was taken to ensure that spectral reflectance sensors were set up at the same viewing angle across all species. This helped to ensure that signal interference due to illumination were minimal.

To eliminate "background effects", sensors were deployed over areas with a monoculture of one species. To ensure that only the canopy of one species at a time was measured, spectral reflectance sensors were deployed close to the canopy. Sensors were deployed ±20 cm above plant canopies to ensure that the FOV of the sensors capture only that specific species reflectance signal. High spatial variability in climate has been documented on Marion Island (le Roux and McGeoch, 2008). Meteorological stations, which were deployed in conjunction with the spectral reflectance sensors, were therefore installed at a similar height as the spectral reflectance sensors to ensure that the meteorological measurements reflect the climate experienced by plant canopies.

PRI measurements have shown to correlate with fluorescence measurements (Fv/Fm, Fs, Fv/Fm') over a wide range of habitat types, including natural and artificial habitats (Dobrowski *et al.* 2005; Garbulsky *et al.* 2011). Fv/Fm' measurements of top canopy leaves or "sun lit" leaves have been shown to have a strong correlation with PRI measurements over a wide variety of species (Gamon *et al.* 1997). Fv/Fm' is a fluorescence measurement of the photochemical efficiency of photosystem Ⅱ (Gamon *et al.* 1997).

There was a significant relationship found between fluorescence measurements (Fv/Fm and Fv/Fm') and PRI measurements, confirming that PRI can be used to asses stress over a variety of plants found on Marion Island. This relationship however can differ significantly between species. This was seen where both positive relationships between Fv/Fm and PRI in both grasses as well as for both the lower plant species were found; however this relationship was not seen for the two cushion plants (*A. selago* and *S. procumbus*).

The difference in canopy structure between the different functional groups can lead to fluorescence measurements made at leaf level not correlating to canopy PRI measurements as seen with the cushion plants. Other wavebands, besides 531 and 570 nm, have been suggested to measure PRI signal at canopy level, since these wavelengths may have significant confounding factors relating to canopy structure such as scattering of light that can affect the signal, besides the pigment changes themselves (Gamon *et al.* 1992; Garbulsky *et al.* 2011).

This study adds to the growing body of literature that PRI provides a measure of light use efficiency and stress associated with photosystem Ⅱ. This has been shown to be true not only within species, but across species of different functional types as well (Gamon *et al.* 1992;

Gamon *et al.* 1997). The importance of canopy measurements of fluorescence in conjunction with PRI measurements gets reiterated by the strength difference in relationship between "sun lit" and "shaded" leaves within a canopy (Gamon *et al.* 1997; Stylinski *et al.* 2002; Garbulsky *et al.* 2011).

Even with the variability in PRI measurements, most studies showed that PRI is still a valuable indicator of plant stress as well as radiation use efficiency across different habitat types and species for both canopy level and leaf level. Most of the discrepancies found with spectral reflectance measurements, are found when canopy level measurements are compared to leaf level measurements (Garbulsky *et al.* 2011). The relationship between fluorescence measurements and PRI measurements were shown to be strongest when sun lit leaves or "top of canopy leaves" were used. Since spectral reflectance sensors have a top down view of the canopy, measurements made can be associated with physiological changes within the canopy itself (Gamon *et al.* 1992; Gamon *et al.* 1997; Stylinski *et al.* 2002; Garbulsky *et al.* 2001).

An inverse relationship between Fv/Fm' and NPQ measurements can be seen across all species. With a decrease in the light use efficiency within photosystem Ⅱ a need to dissipate excessive light energy will exist and is reflected through NPQ (Rohaecek, 2002; Bilger *et al.* 2016).

Changes in the xanthophyll cycle pigments are associated with NPQ. This photo-protective mechanism can be indicative of the psi PS Ⅱ, since the need to dissipate light energy will increase as psi PS Ⅱ decreases (Demmig-Adams and Adams, 1996). NPQ measurements have been shown to be closely linked to PRI measurements at leaf level (Stylinski *et al.* 2002; Gou and Trotter, 2006). There was no relationship however found between PRI measurements and NPQ measurements in any of the species sampled in this study. This may be a result of leaf-angle light distribution. PRI measurements were made at canopy level, while NPQ measurements were made at leaf level. Discrepancies therefore arises and has been documented in other studies as well (Garbulsky *et al.* 2001).

During this study single sites were chosen to be representative of other individuals of the same species in the surrounding area. It is important to establish that the point measurements of spectral reflectance sensors in the field are a true reflection of surrounding individuals.

When light energy exceeds the capacity of photosystem Ⅱ a photo-protective mechanism, like the xanthophyll cycle, will be activated (Barton and North, 2001; Gamon, 2011; Garbulsky *et al.* 2011). By understanding the yield of photosystem Ⅱ under stable conditions, we can determine whether different individuals of plants or species have different capacities of light

use efficiency (Gamon *et al.* 1997). The photosynthetic yield of photosystem Ⅱ was therefore measured to determine whether measurements of individual canopies per species will be representative of individuals of the same species in the surrounding area. Caution was applied to ensure that all measurements were made under a constant light source and temperature to ensure that no external stress factors influenced the light use efficiency of photosystem Ⅱ. Stress relating to water loss experienced during the study was accounted for, by weighing each individual before and after each measurement.

The photosynthetic yield measured was not significantly different between individuals of the same species when measured under similar and stable environmental conditions. There was a difference between the photosynthetic yield of photosystem Ⅱ measured between different species and functional groups. This was indicative that remote sensing measurements of single sites (canopies) in the field can be representative of individuals of the same species in the surrounding area, since the yield of photosystem Ⅱ was similar between individuals of the same species under stable conditions.

The difference seen in the psi PS Ⅱ measurements between different species shows the variability in photosynthetic capacity across species. This difference between species was also seen between different functional groups, highlighting that assumptions about physiological responses cannot be made across functional groups.

These laboratory based measurements confirm the idea that spectral reflectance measurements of single individuals can be indicative of the behaviour of a species in general and is not just isolated to the individual itself. The spectral reflectance measurements in the laboratory made under stable conditions reflects this, with the signal not being significantly different between individuals of the same species.

Throughout the literature PRI measurements accounted for the physiological responses of plants at not only leaf level, but canopy level as well. PRI measurements have been used at various temporal scales (from hourly to seasonally) to determine light use efficiency and environmental stress decreasing production (Garbulsky *et al.* 2011). The xanthophyll cycle can have a rapid response to environmental change, influencing spectral reflectance measurements (Magney *et al.* 2016). Coarse resolution measurements leave space for doubt since it can be difficult to determine whether the response seen is a true reflection of the physiological changes in the plant or if it is rather a relic of the measurement time. By increasing the resolution of the PRI measurements, we can decrease this doubt and get a true picture of the rapid physiological changes in the plant (Magney *et al.* 2016). By measuring at

such a high resolution over the span of various seasons, new insight can be gained about the physiological changes of plant functional types on a seasonal scale as well as on a diurnal scale during different changes in season.

4.7. Conclusions

The use of PRI as a measure of physiological changes shows great promise for determining photosynthetic, production and stress patterns within different plant functional groups. The deployment of *in situ* sensors can be useful to supplement meteorological and environmental data to help with the modelling of production rates. These measurements can however often be misleading. By showing that PRI measurements are an indicator of physiological stress, discrepancies that might arise due to light and/or signal interference can be eliminated. This study therefore forms part of the growing body of literature confirming the effective use of PRI measurements in the field to determine physiological patterns within plants. This study also highlights the effectiveness of using single sites as a representation of the surrounding area.

5. Physiological response of key functional types on a Sub-Antarctic Island in response to diurnal environmental change

5.1. Abstract

Much attention has been given to determining the seasonal drivers of production, with few studies focussing on diurnal drivers of plant physiological patterns on Marion Island. Environmental variability on a diurnal timescale can have a significant influence on production rates, if efficient photosynthetic rates cannot be established during the day. Diurnal PRI patterns are a direct reflection of physiological stress experienced during the day in relation to changing environmental variables. This study therefore focussed on determining the environmental drivers of diurnal PRI patterns of different plant functional types. There was a significant difference seen in diurnal PRI patterns for different plant functional types, with lower plant species often having the lowest PRI ranges with the deepest midday PRI depression seen. A midday PRI depression was seen for all species, except for *A. selago* and *S. procumbus* where this pattern was not seen on cold and warm, calm days. The diurnal PRI patterns seemed to follow the expected diurnal PRI pattern where the deepest depression occurring at the highest air temperature and VPD measurements. The exception to this was *A. selago* and *S. procumbus*. Wind as a diurnal driver was highlighted with wind having both a positive and negative role, by either decreasing canopy temperatures on warm days that exceeded temperature optima of plants or increasing water loss in lower plant species. The importance of variability in the physiological response between different plant functional types was also highlighted, with segregation in PRI response seen between different functional groups.

5.2. Introduction

Little is known about the diurnal physiological patterns influencing production on Marion Island with the historical focus rather being on annual production rates (Smith 1987a, b, c, d). Annual production on Marion Island is well below the estimated production rates (Lieth, 1973). Much attention has been given to understanding seasonal environmental drivers influencing production systems in both Arctic and sub-Antarctic tundra systems, with little emphasis put on the diurnal physiological patterns of plants. PRI measured on a diurnal scale is the reflection of excessive light energy in response to stress limiting photosynthetic activity within a plant (Gamon *et al.* 1997). Diurnal stress can therefore play a significant role in decreasing plant primary production.

Low radiation levels, due to the presence of cloud cover, has been proposed to be the main driver for low production rates on Marion Island, with cloud cover limiting both the intensity and the duration of incoming solar irradiance levels (Smith 1987d). High irradiance levels can occur at virtually any time of the day, due to cloud movement (Schulze, 1971).Wind speeds have also been hypothesized to influence production on the island, with wind speed patterns changing drastically on a diurnal scale (Schulze, 1971). High wind speeds are thought to suppress stomatal conductance (Smith and Steenkamp, 2001), but this has not been studied *in situ*. Other variables that may influence production, such as VPD and air temperature, have not been studied fully, with proposed variables limiting production only hypothesized, but not tested.

With the development of new spectral reflectance sensors, the possibility of measuring *in situ* physiological responses of plants to environmental variability has been made possible (Garbulsky *et al*. 2011). Very little is known about the in-field physiological behaviour of sub-Antarctic species and distinct patterns of production can be seen in different communities (Smith, 1987a, b, c, d).

The aim of this chapter is to determine patterns of physiological stress and photosynthetic performance in relation to environmental variables. This chapter will investigate what drives these patterns of physiological stress and photosynthetic performance on a diurnal scale. The second aim will focus on whether these patterns of physiological stress and performance are different for different functional groups. The chapter will also determine how different functional groups respond to different environmental changes.

5.3.Data analysis

To understand the influence of environmental variables on the diurnal physiological response of the plant, it was necessary to reduce a very large data set to a manageable set for analysis. For this reason, an analysis was performed to cluster the large number of diurnal responses into clusters of archetypal diurnal patterns based on the measured climate variables. A k-means clustering procedure was used. Daily means of all variables were used for the cluster analysis. Air temperature and soil temperature minima and maxima for each day were also included to account for diurnal temperature variability. Days where data were missing due to either system failure, or variables exceeding ranges of sensors were excluded from the analysis (less than 5%). All night time (solar irradiance < 0) measurements were excluded from the analysis, since spectral reflectance measurements cannot be measured without incoming solar irradiance.

To determine the number of clusters, a Principal Component Analysis (PCA) was used to determine the overall differences in days based on their environmental and climatic variables measured. The number of clusters was determined based on the number of principal components that was needed to explain more than 85% of the variation. Scaling was corrected for the dataset to ensure that the variances across all the variables were uniform before running the PCA. Diurnal archetypes, as determined by the clusters, were then characterized by their distinguishing biophysical characteristics.

A generalised mixed linear model (GLM) with Gaussian distribution was used to determine the effect of different environmental variables (or combination of variables) for both PRI and canopy temperature measured for all species within each cluster. The fixed effects variables were air temperature, soil temperature, solar irradiance, VPD, atmospheric pressure, relative humidity wind speed and soil water. Collinearity between all variables was tested for and excluded from the analysis as fixed effects if collinearity was found.

A second order Akaike's Information Criterion (AIC) was applied to determine which variables (or combinations) had the highest influence in PRI and canopy temperatures within each cluster respectfully. Maximised log likelihoods, model weights and AIC differences were determined for each model. A null model for both PRI and canopy temperature was included in the mixed models to determine if the variation seen in both canopy temperature and PRI measured are a reflection of changes in environmental variables as opposed to a variable that was not measured. This was done for all species independently.

The diurnal average of hourly values was determined within each cluster per species across all variables to determine the diurnal pattern of the vegetation indexes and environmental variables. PRI and canopy temperatures were not normally distributed. A Kruskal-Wallis ANOVA was therefore used to compare the hourly diurnal patterns of both PRI and canopy temperatures between clusters within all species.

Pearson correlation was used to determine if there was any relationship between the vegetation indexes (PRI and canopy temperature). The correlation was done between the vegetation indexes and all other environmental variables using the mean hourly values within each cluster.

5.4. Results

5.4.1. Characterizing diurnal archetypes based on biophysical variables

Days were clustered into four distinct diurnal archetypes and then characterized based on their biophysical variables. The first four components of the PCA explained more than 85% of the

variability, with component one explaining 47% and cumulatively 68% with component two (Table 5.1). Based on the PCA the variables with the highest loadings in the components explaining more than 85% of the variability were solar irradiance and air temperature (Table 5.2 and Figure 5.1).

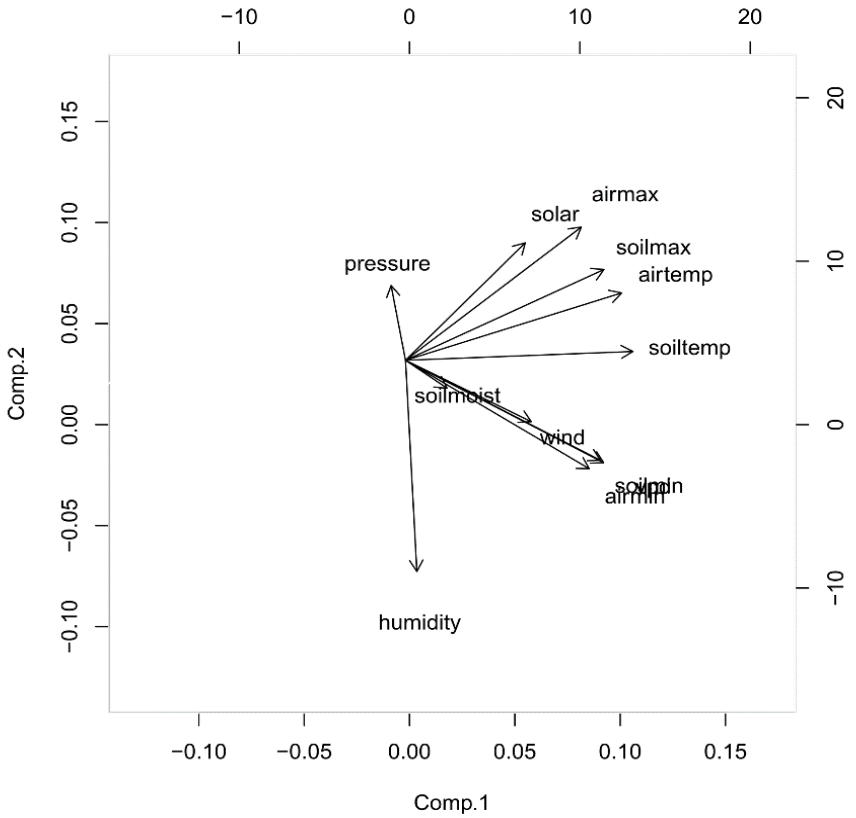

Figure 5.1 Biplot for principal component 1 and 2 yielded by the PCA of the environmental variables measure per day (Cumalative variability explaind by principla component 1 and 2 is 68.4%

Table 5.1 Standard deviation, Proportion of variance and cumulative proportion of components in PCA, based on environmental variables, explaining more than 85% of the variability.

	Component 1	Component 2	Component 3	Component 4
Standard deviation	2.349	1.603	1.252	0.696
Proportion of variance	0.469	0.215	0.131	0.040
Cumulative proportion	0.469	0.684	0.816	0.921

Table 5.2 Loadings of each environmental variable used in PCA to the different components, explaining more than 85% of the variability.

	Component 1	Component 2	Component 3	Component 4
Solar irradiance	0.214	0.324	-0.316	0.358
Air temperature	0.387	0.186	0.086	-0.029
Soil temperature	0.407	0.024	0.099	-0.139
Soil water	0.074	-0.077	-0.660	-0161
Atmospheric pressure	-0.026	0.206	0.617	0.296
Wind	0.225	-0.169	-0.162	0.826
VPD	0.355	-0.283	0.082	-0.031
Relative humidity	0.020	-0.583	0.023	0.029

The days were clustered into day archetypes based on the PCA results (Figure 5.2).

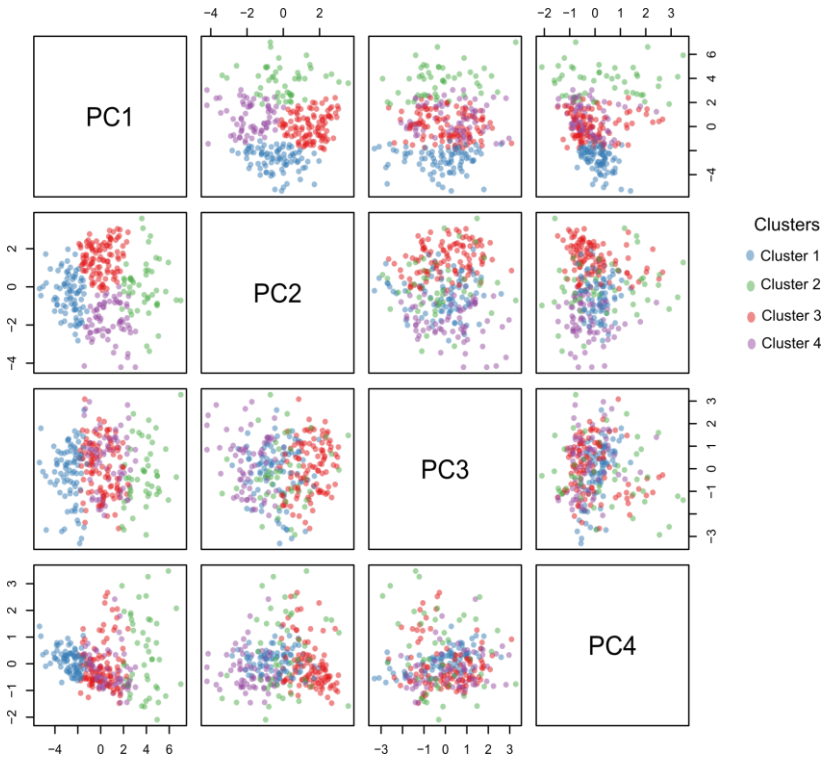

Figure 5.2 First four components of PCA that together explain 85% of the variability. Colour coding of days grouped together by diurnal archetype based on k-means clusters in each component.

The four different diurnal archetypes based on the clusters can be characterized according to their biophysical variables as following (Figure 5.3 - 5.10):

Cluster 1: Warm, windy days

This diurnal archetype is defined by average wind speeds of more than 15 m/s and high temperatures, with average air temperatures being more than 12°C and average soil temperatures being >11°C. This cluster has the highest solar irradiance levels with average solar irradiance being more than 400 $W.m^2$. This high input of energy is associated with higher temperatures which can be seen in this cluster. Average atmospheric pressure is between 100 and 101 kPa which is indicative of median annual pressure at sea level. Average relative humidity is high, ranging between 80% and 90%. The high relative humidity and air temperatures are reflected in the VPD, with this cluster having the average highest VPD of 1.1 (kPa).

Cluster 2: Warm, calm days

This diurnal archetype is characterized by low solar irradiance levels, with average solar irradiance levels being less than 200 $W.m^2$. The low solar irradiance is an indication of greater cloud cover. The average relative humidity in this cluster is higher than in any other cluster with an average of more than 90%. This can be associated with the higher cloud cover contributing to more precipitation as mist or rain. The average air temperatures are 7°C with similar average soil temperatures ranging between 6 to 7°C. Average atmospheric pressure are between 100 and 101 kPa which is expected of areas close to sea level. Wind speeds are on average ranging between 6 – 7 m/s. Average VPD ranges between 0.9 and 1.1 kPa.

Cluster 3: Cold, calm days

This diurnal archetype is defined by what is often termed "good weather". Average atmospheric pressure is high with an average of more than 101 kPa which is traditionally associated with cold, calm days. Low wind speeds with an average of less than 5 m/s are experienced on these days. Average humidity is 70% with an average VPD of just over 0.8 (kPa). Temperatures are not at either end of the extremes (cold or hot), but are mild with average air temperature ranging between 8 to 11°C and average soil temperatures ranging between 7 to 9°C. Average solar irradiance are between 300 and 400 $W.m^2$.

Cluster 4: Cold, cloudy days

This diurnal archetype is characterized by cold days with average air temperatures being just over 5°C and average soil temperatures being less than 5°C. Solar irradiance levels are also low with average incoming solar irradiance levels being roughly 200 $W.m^2$. Average

atmospheric pressure ranges between 100 and 101 kPa which is expected of areas close to sea level. Relative humidity is 80% with VPD being at its lowest with an average of 0.7 kPa. Wind speeds are low in this cluster with average wind speeds being less than 5 m/s.

Overall, it is important to note that soil water was not significantly different between any of the clusters and therefore had no significant effect on defining clusters.

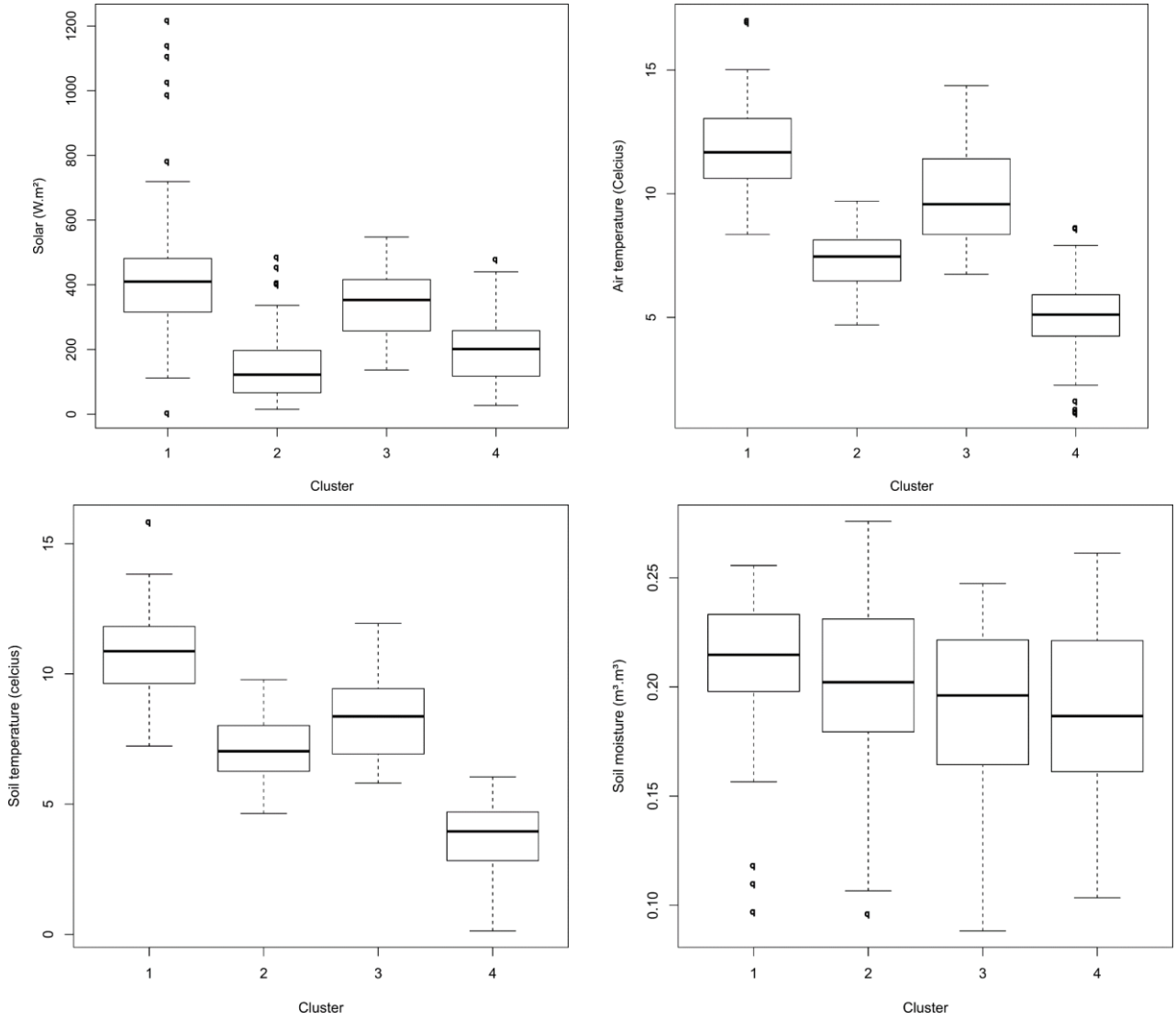

Figure 5.3-5.6 Box and whisker plot of 5.3) solar irradiance, 5.4) air temperature, 5.5), soil temperature and 5.6) soil water of each day archetypes

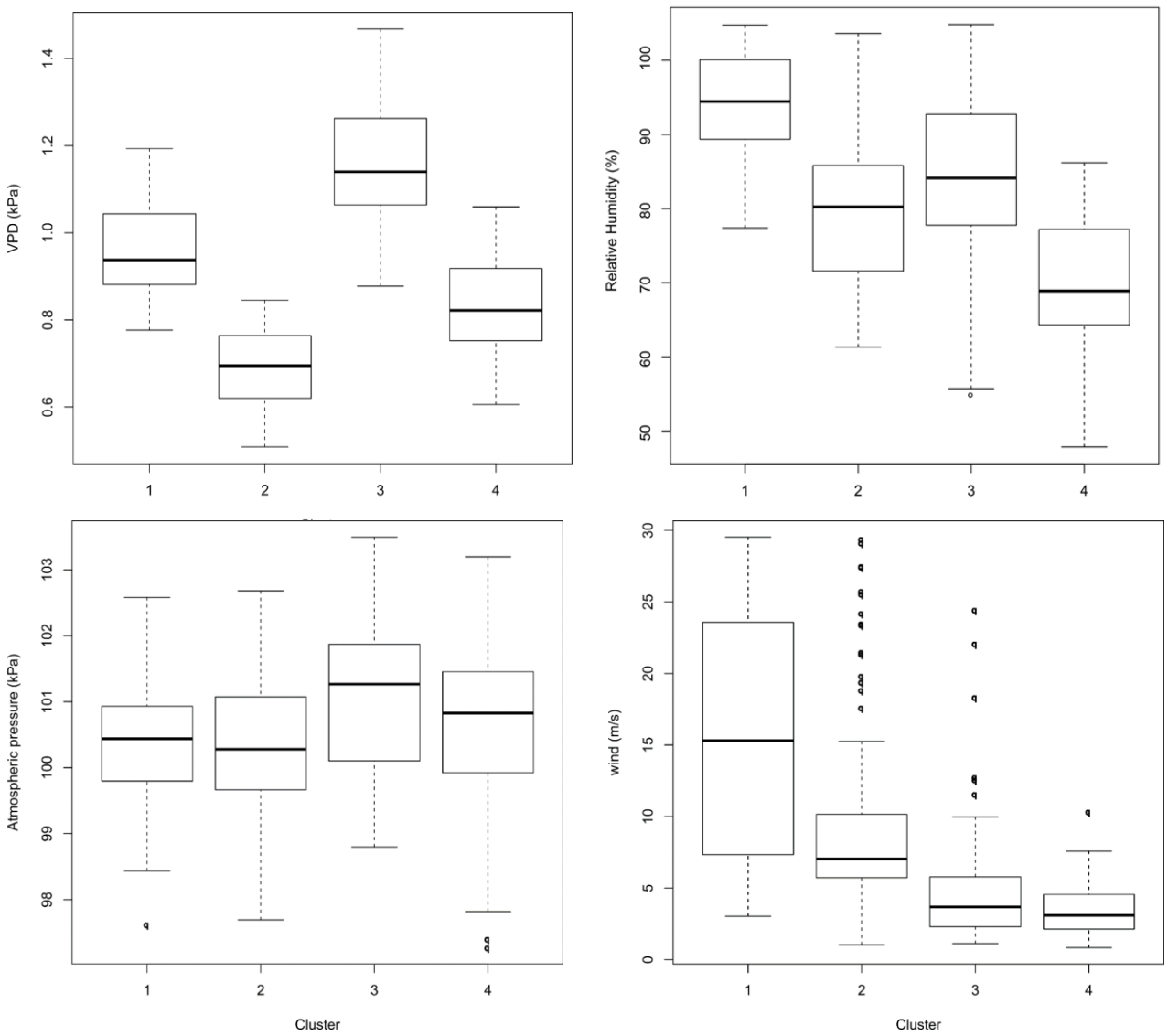

Figure 5.7-5.10 Box and whisker plot of 5.7) VPD, 5.8) relative humidity, 5.9), atmospheric pressure and 5.10) wind of each day archetypes

5.4.2. Diurnal patterns of PRI

Figures 5.11 to 5.16 shows the diurnal response of all the species within the different diurnal archetypes. From a visual inspection the PRI diurnal response curves of the lower plant species (*R. lanuginosum* and *S. colerata*) has an inverse relationship with solar irradiance, with a decrease in PRI at peak solar irradiance, irrespective of the average solar irradiance experienced during the different types of days. The diurnal response of lower plant species follow the expected pattern, where the deepest photosynthetic depression coincides with the highest air temperature and VPD measurements. A midday depression in PRI measurements for the cushion plants (*A. selago* and *S. procumbus*) can be seen only in days with high solar irradiance. In days with low solar irradiance, the PRI diurnal pattern of both cushion plants parallels the solar irradiance pattern with only a slight levelling off at peak irradiance. The predicted diurnal PRI pattern, where the lowest PRI measurements coincide with maximum air temperatures and VPD, can be seen only on days with high temperatures for cushion plants. Midday PRI depression can be seen in both grasses (*A. magellanica* and *A. stolonifera*), coinciding with peak solar irradiance. The PRI depression of grasses also coincides with the highest VPD and air temperature.

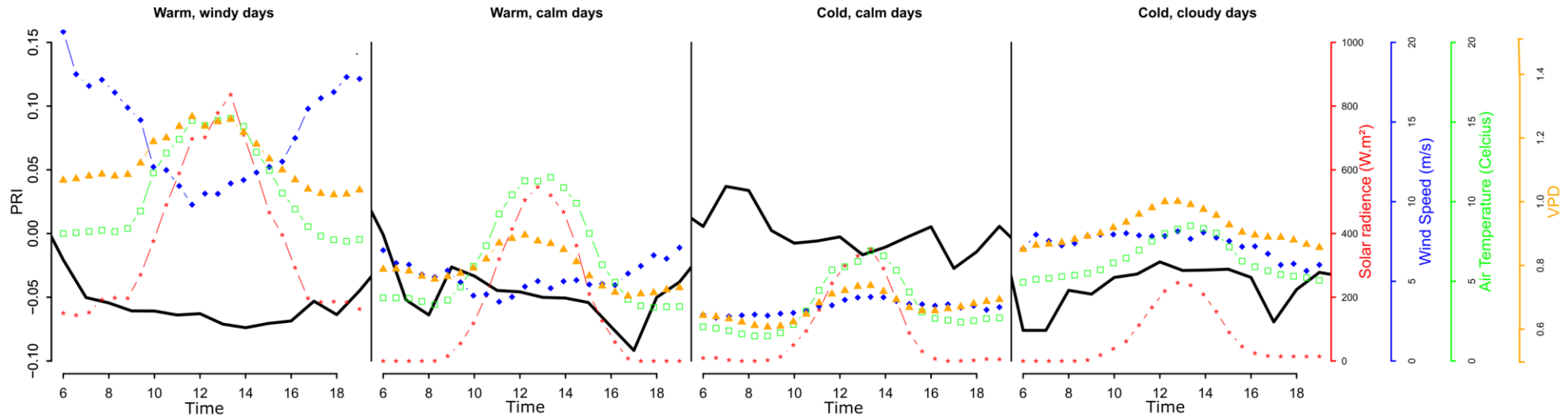

Figure 5.11 Diurnal pattern of *A. selago* on the different diurnal archetypes. PRI signal compared with solar irradiance (red asterisks), wind (blue solid dots), air temperature (green squares) and VPD (yellow triangles). PRI response represented by solid line.

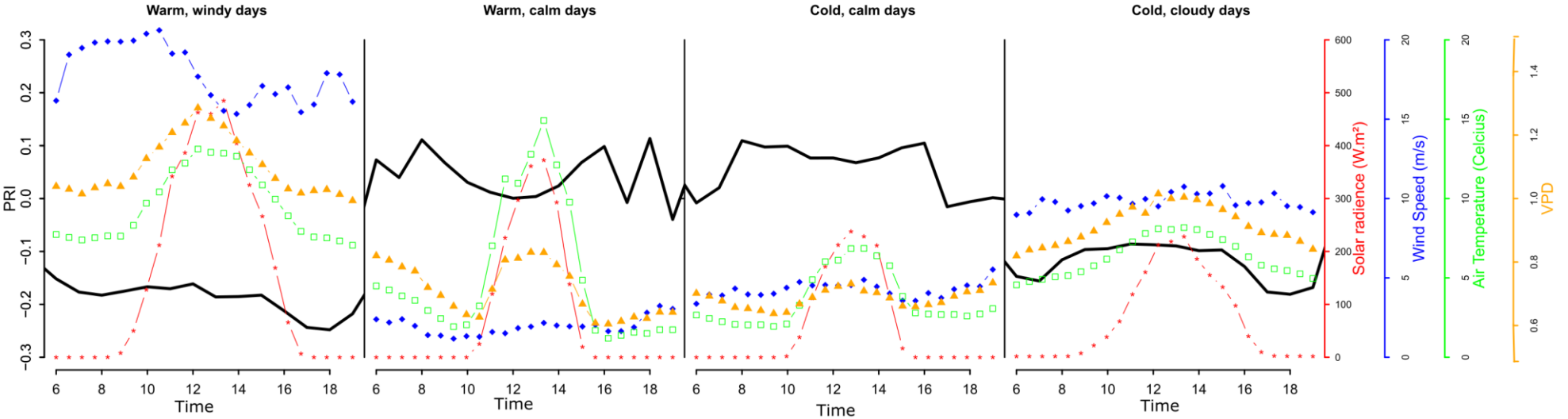

Figure 5.12 Diurnal pattern of *S. procumbus* on the different diurnal archetype. PRI signal compared with solar irradiance (red asterisks), wind (blue solid dots), air temperature (green circles) and VPD (yellow triangles). PRI response represented by solid line.

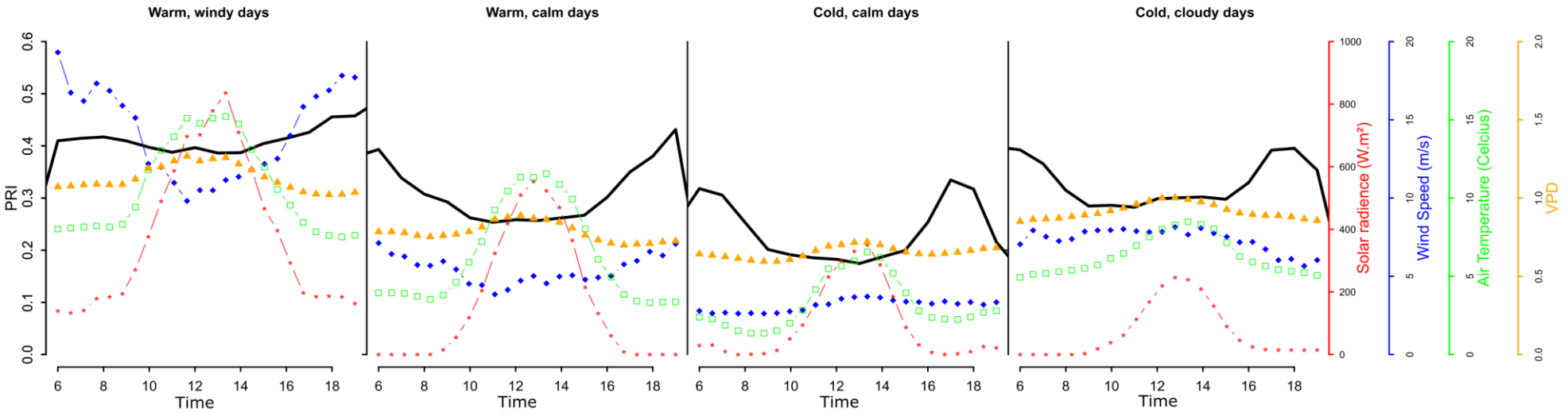

Figure 5.13 Diurnal pattern of *A. magellanica* on the different types of days. PRI signal compared with solar irradiance (red asterisks), wind (blue solid dots), air temperature (green square) and VPD (yellow triangles). PRI response represented by solid blackline.

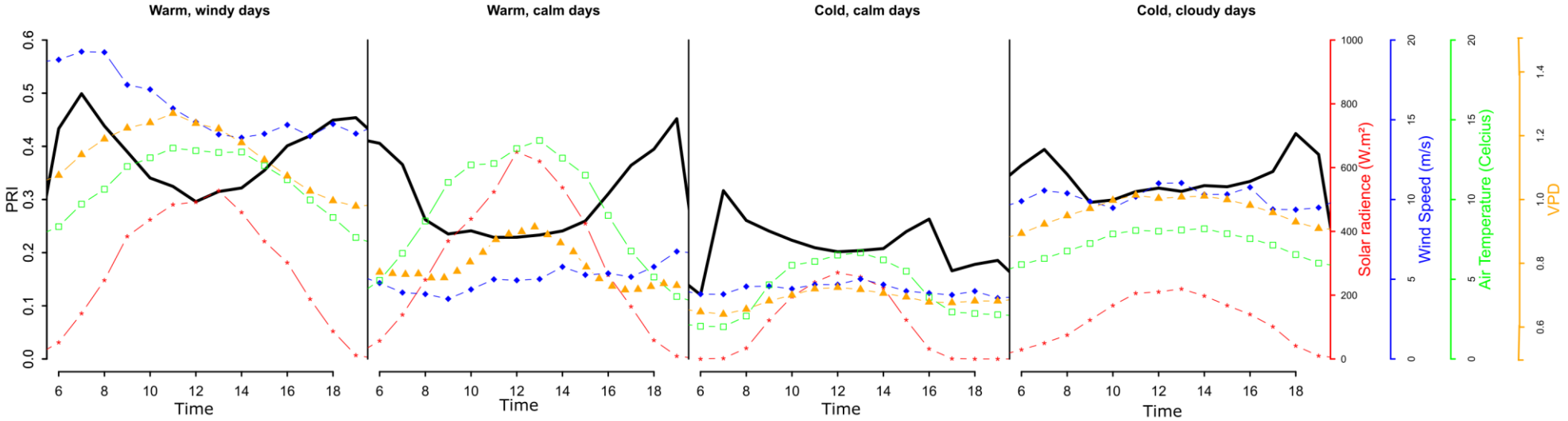

Figure 5.14 Diurnal pattern of *A. stolonifera* on the different types of days. PRI signal compared with solar irradiance (red asterisks), wind (blue solid dots), air temperature (green squares) and VPD (yellow triangles). PRI response represented by solid line.

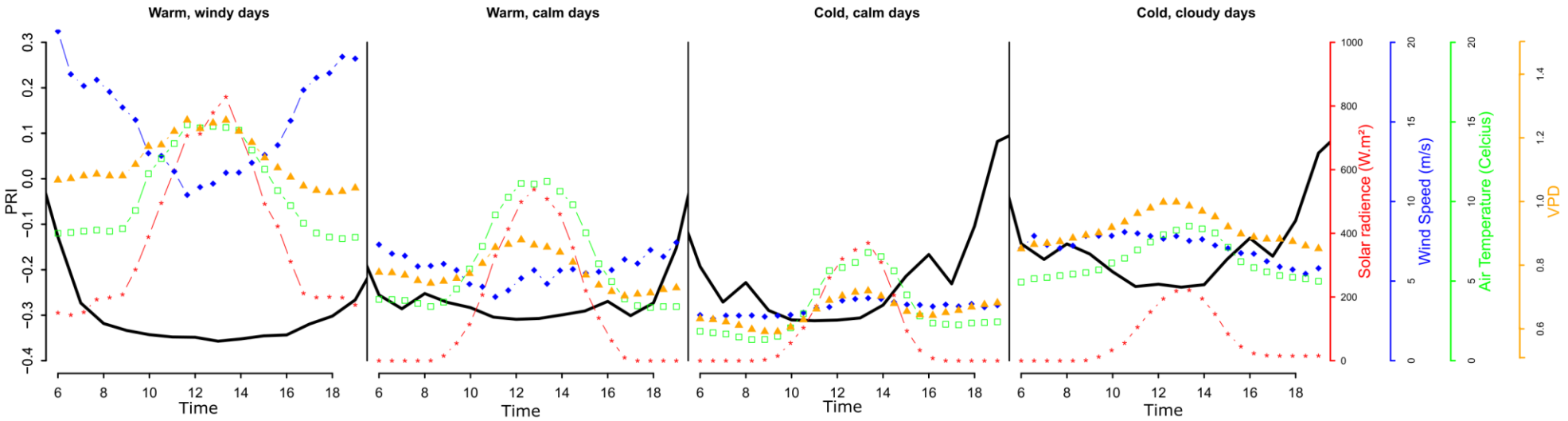

Figure 5.15 Diurnal pattern of *R. lanuginosum* on the different types of days. PRI signal compared with solar irradiance (red asterisks), wind (blue solid dots), air temperature (green squares) and VPD (yellow triangles). PRI response represented by solid line.

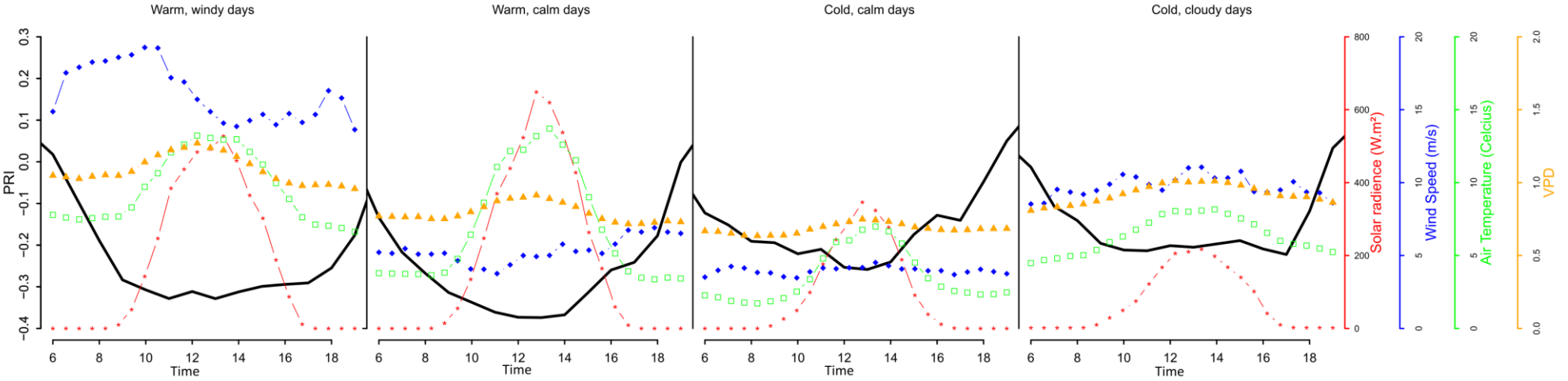

Figure 5.16 Diurnal pattern of *S. colerata* on the different types of days. PRI signal compared with solar irradiance (red asterisks), wind (blue solid dots), air temperature (greensquares) and VPD (yellow triangles). PRI response represented by solid line.

5.4.3. Comparison of vegetation indexes between the four types of days

The Kruskal-Wallis test revealed that there was no significant difference of PRI measurements made for *A. selago* between different types of days (Kruskal-Wallis: H = 7.306, n = 96, p > 0.5). A post-hoc test however showed that there was one significant difference in PRI measurements made for *A. selago*, between warm, windy days (cluster 1) and cold, calm days (cluster 3) (t-test: z = 2.689, p < 0.05). The Kruskall-Wallis test showed that there was a significant difference in canopy temperatures measured between different types of days for *A. selago* (Kruskal-Wallis: H = 36.634, n = 96, p < 0.05). Canopy temperatures of *A. selago* measured on warm, windy days (cluster 1) were significantly different from all the other types of days (Table 5.3).

Table 5.3 Kruskal-Wallis ANOVA results comparing both PRI and canopy temperatures between different types of days for *A. selago* (values represent z values) (* = p values significant).

PRI				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	1.549	-	-	-
Cold, calm days	**2.689***	1.139	-	-
Cold, cloudy days	1.523	0.026	1.166	-
Canopy temperatures				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	**5.042***	-	-	-
Cold, calm days	**5.129***	0.088	-	-
Cold, cloudy days	**4.586***	0.456	0.544	-

There was a significant difference in PRI measurements of *S. procumbus* between different types of days (Kruskal-Wallis: H = 38.889, n = 96, p < 0.05). The post-hoc test revealed that PRI measurements made on cold, calm days and cold, cloudy days were not significantly different. PRI measurements made on warm, windy days and cold, cloudy days were also not significantly different (Table 5.4). There was a significant difference between canopy temperatures of *S. procumbus* between the different types of days (Kruskal-Wallis: H = 58.043, n = 96, p < 0.5). Similar results were seen in canopy temperatures than in the PRI measurements for *S. procumbus*, with the post-hoc test revealing the same days not being significantly different (Table 5.4).

Table 5.4 Kruskal-Wallis ANOVA results comparing both PRI and canopy temperatures between different types of days for *S. procumbus* (values represent z values) (* = p values significant).

PRI				
	Warm, windy days	**Warm, calm days**	**Warm, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	**4.814***	-	-	-
Cold, calm days	**4596***	0.218	-	-
Cold, cloudy days	0.642	**4.171***	**3.953***	-
Canopy temperatures				
	Warm, windy days	**Warm, calm days**	**Warm, calm days**	**Cold, cloudy days**
Warm, windy days	-		-	-
Warm, calm days	**5.891***	-	-	-
Cold, calm days	**6.699***	0.808	-	-
Cold, cloudy days	2.456	**3.435***	**4.244***	-

There was a significant difference between PRI measurements made for *A. magellanica* between the different type of days (Kruskal-Wallis: H = 12.819, n = 96, p < 0.05). The post-hoc showed that the PRI measurements were only significantly different between cold, cloudy days and warm, windy days (Table 5.5). There was a significant difference between canopy temperatures measured for *A. magellanica* between different types of days (Kruskal-Wallis: H = 69.205, n = 96, p <0.05). The post-hoc showed that the canopy temperatures measured on warm, windy days and cold, cloudy days were not significantly different (Table 5.5).

Table 5.5 Kruskal-Wallis ANOVA results comparing both PRI and canopy temperatures between different types of days for *A. magellanica* (values represent z values) (* = p values significant).

PRI				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	2.0467	-	-	-
Cold, calm days	**3.544***	1.497	-	-
Cold, cloudy days	1.539	0.508	2.005	-
Canopy temperatures				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	**4.301***	-	-	-
Cold, calm days	**8.285***	**3.985***	-	-
Cold, cloudy days	**3.601***	0.699	**4.684***	-

The Kruskal-Wallis test showed that there was no significant difference between PRI measurements made for *A. stolonifera* between different types of days (Kruskal-Wallis: H = 12.049, n = 96, $p < 0.05$). The post-hoc however showed that only PRI measurements made on warm, windy days and cold, calm days were significantly different (Table 5.6). There was a significant difference in canopy temperatures measured of *A. stolonifera* between the different types of days (Kruskal-Wallis: H = 57.73, n = 96, $p < 0.05$). The post-hoc showed that only the canopy temperatures measured on warm, windy days and cold, cloudy days were not significantly different (Table 5.6).

Table 5.6 Kruskal-Wallis ANOVA results comparing both PRI and canopy temperatures between different types of days for *A. stolonifera* (values represent z values) (* = p values significant).

PRI				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	1.026	-	-	-
Cold, calm days	**3.279***	2.254	-	-
Cold, cloudy days	0.709	0.316	2.569	-
Canopy temperatures				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	**3.736***	-	-	-
Cold, calm days	**7.487***	**3.751***	-	-
Cold, cloudy days	**2.684***	1.052	**4.803***	-

There was no significant difference in PRI measurements of *R. lanuginosum* between different types of days (Kruskal-Wallis: H = 7.671, n = 96, p > 0.05). Canopy temperatures measured for *R. lanuginosum* were however significantly different (Kruskal-Wallis: H: 58.983, n = 96, p < 0.05). The post- hoc showed that only canopy temperatures measured between cold, cloudy days and warm, windy days did not differ significantly (Table 5.7).

Table 5.7 Kruskal-Wallis ANOVA results comparing both PRI and canopy temperatures between different types of days for *R. lanuginosum* (values represent z values) (* = p values significant).

PRI				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	0.637	-	-	-
Cold, calm days	1.472	0.834	-	-
Cold, cloudy days	2.617	1.979	1.145	-
Canopy temperatures				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	**3.953***	-	-	-
Cold, calm days	**7.668***	**3.715***	-	-
Cold, cloudy days	**3.549***	0.404	**4.119***	-

The Kruskal-Wallis test showed that there was no significant difference in PRI measurements made for *S. collerata* between different types of days (Kruskal-Wallis: H = 5.285, n = 96, p > 0.05). There was a significant difference between canopy temperatures measured for *S. collerata* between different types of days (Kruskal-Wallis: H = 45.984, n = 96, p < 0.05). The post-hoc showed that canopy temperatures on cold, cloudy days and warm, windy days were not significantly different, as well as canopy temperatures measured on cold, cloudy days and warm, calm days (Table 5.8).

Table 5.8 Kruskal-Wallis ANOVA results comparing both PRI and canopy temperatures between different types of days for *S. collerata* (values represent z values) (* = p values significant).

PRI				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	0.544	-	-	-
Cold, calm days	1.176	1.720	-	-
Cold, cloudy days	1.419	1.964	0.244	-
Canopy temperatures				
	Warm, windy days	**Warm, calm days**	**Cold, calm days**	**Cold, cloudy days**
Warm, windy days	-	-	-	-
Warm, calm days	**3.010***	-	-	-
Cold, calm days	**6.715***	**3.705***	-	-
Cold, cloudy days	2.544	0.466	**4.171***	-

5.4.4. Diurnal environmental drivers of vegetation indexes

To understand how environmental variables interact and drives changes in PRI and canopy temperature measurements, AIC values were used to determine the model of best fit within each day archetype for each species. In cases where the null model was the model of best fit, the second model of best fit was also given. Twenty four different models were included in the analysis based on different combinations of variables. A list of models used is given in Table 5.9.

Table 5.9 Model name and model number used in GLM to determine diurnal patterns.

Model number	Model
1	Null model
2	Relative humidity
3	Soil water
4	Solar irradiance
5	Solar irradiance + Soil water
6	Air temperature + Soil water
7	Air temperature + Relative humidity
8	Air temperature + Solar irradiance
9	Air temperature
10	Wind speed + Solar irradiance +Soil water
11	Wind speeds + Air temperature
12	Wind speed + Solar irradiance + Soil water
13	Wind speed + Solar irradiance + relative humidity
14	Wind speed + Solar irradiance + Air temperature
15	Wind speed + Relative humidity
16	Wind speed + Soil water
17	Wind + Soil water
18	VPD
19	Wind speed + VPD
20	Wind speed + Solar irradiance + VPD
21	Air temperature + VPD
22	Solar irradiance + VPD
23	Wind speed + Air temperature + VPD

A general overview of models of best fit within each "type" of day for each species is given in Tables 5.10 – 5.17.

Warm, windy days

On warm, windy days the null model was selected for the model of best fit for driving canopy temperatures for *A. selago*. The second model of best fit was therefore also given, indicating that an interaction of solar irradiance and VPD had the highest influence on canopy temperatures of *A. selago*. Both solar irradiance and soil water had the highest influence in driving PRI measurements in *A. selago* on warm, windy days.

An interaction between wind speed, air temperature and soil water had the highest effect in driving canopy temperatures of *S. procumbus*. The null model was the model of best fit for influencing PRI measurements for *S. procumbus*. The second model of best fit was therefore also reported, indicating that PRI measurements were most influenced by wind speeds, air temperatures and soil water.

The null model was selected for influencing canopy temperatures for *A. magellanica*. The second model of best fit was therefore also reported, indicating that wind speed and VPD had a significant influence in determining canopy temperatures of *A. magellanica*. A combination of changes in solar irradiance and soil water had the highest influence in determining PRI measurements for *A. magellanica.*

An interaction between wind speed, solar irradiance and VPD had the highest influence in determining canopy temperatures in *A. stolonifera*. An interaction between air temperature and relative humidity had the highest effect on driving PRI measurements for *A. stolonifera* on warm, windy days.

For *R. lanuginosum* the null model was selected as the model of best fit for determining canopy temperatures. The second model of best fit was therefore also reported, indicating that the interaction between solar irradiance and VPD had a significant effect on canopy temperatures of *R. lanuginosum*. The combination of air temperature and solar irradiance had the highest influence on PRI measurements for *R. lanuginosum*.

The combination of solar irradiance and VPD was the model of best fit for driving canopy temperatures for *S. colerata*. Solar irradiance and VPD was the model of best fit influencing PRI measurements for *S. colerata* on warm, windy days.

Table 5.10 GLM model section explaining canopy temperatures in warm, windy days (cluster 1) within each species. Logliks (loglikelihood), K (number of parameters), w_i (Akaike weight value), ΔAIC (the model AIC value). If the model of best fit were a null model, the second model of best fit within that cluster was also given.

Species	Model of best fit	Logliks	K	w_i	ΔAIC
A. selago	a) Null model	-637.343	2	1	0
A. selago	b) Solar irradiance + VPD	4386.178	5	1.621	593.101
S. procumbus	Wind speed + Air temperature + Soil water	4251.917	5	<0.001	0
A. magellanica	a) Null model	-605.444	2	1	0
A. magellanica	b) Wind speed + VPD	4940.817	5	<0.001	522.191
A. stolonifera	Wind speed + Solar irradiance + VPD	-783.541	4	1	0
R. lanuginosum	a) Null model	-149.738	2	1	0
R. lanuginosum	b) Solar irradiance + VPD	3669.179	5	<0.001	83.933
S. colerata	Solar irradiance + VPD	3671.722	5	0.926	0

Table 5.11 GLM model section explaining PRI in warm, windy days (cluster 1) within each species. Logliks (loglikelihood), K (number of parameters), w_i (Akaike weight value), ΔAIC (the model AIC value). If the model of best fit were a null model, the second model of best fit within that cluster was also given.

Species	Model of best fit	Logliks	K	w_i	ΔAIC
A. selago	Solar irradiance + Soil water	-725.513	4	0.999	0
S. procumbus	a) Null model	-1407.446	2	1	0
S. procumbus	b) Wind speed + Air temperature + Soil water	-1197.124	5	<0.001	216.322
A. magellanica	Solar irradiance + Soil water	-686.008	4	0.999	0
A. stolonifera	Air temperature + Relative humidity	-331.165	4	0.999	0
R. lanuginosum	Air temperature + Solar irradiance	-408.204	4	1	0
S. colerata	Solar irradiance + VPD	-210.815	5	0.925	0

Warm, calm days

Canopy temperatures of *A. selaga* was most influenced by solar irradiance and VPD on warm, calm days. The same combination of variables had the highest influence on PRI measurements than canopy temperature measurements for *A. selago* on warm, calm days.

A combination of wind speed, air temperature and soil water was the most significant drivers for canopy temperatures of *S. procumbus*. A combination of solar irradiance and soil water had the highest effect on PRI measurements of *S. procumbus*.

The model of wind speed, air temperature and soil water had the highest significance for predicting canopy temperatures for *A. magellanica*. A combination of wind speed, solar irradiance and relative humidity had the highest effect on PRI measurements of *A. magellanica* on warm, calm days.

A. stolonifera's canopy temperatures were driven by a combination of wind speeds, air temperature and relative humidity. The model of best fit determining PRI measurements for *A. stolonifera* was air temperature and soil water.

A combination of wind speed, air temperature and relative humidity had the highest influence in determining canopy temperatures for *R. lanuginosum*. Similar drivers for determining PRI measurements were seen for *R. lanuginosum* than for canopy temperatures, with the model of best fit being wind speed and relative humidity.

Canopy temperatures of *S. colerata* were mostly driven by wind speeds, air temperatures and soil water. The same model of best fit determining canopy temperatures were also seen determining PRI measurements of *S. colerata* on warm, calm days.

Table 5.12 GLM model section explaining canopy temperatures in warm, calm days (cluster 2) within each species. Logliks (loglikelihood), K (number of parameters), w_i (Akaike weight value), ΔAIC (the model AIC value). If the model of best fit were a null model, the second model of best fit within that cluster was also given.

Species	Model of best fit	Logliks	K	w_i	ΔAIC
A. selago	Solar irradiance + VPD	5507.195	5	0.999	0
S. procumbus	Wind speed + Air temperature + Soil water	-873.607	5	1	0
A. magellanica	Wind speed + Air temperature + Soil water	-1195.979	5	0.909	0
A. stolonifera	Wind speed + Air temperature + Relative humidity	-70.263	5	0.999	0
R. lanuginosum	Wind speed + Air temperature + Relative humidity	-1110.961	5	0.999	0
S. colerata	Wind speed + Air temperature + Soil water	-710.423	5	0.999	0

Table 5.13 GLM model section explaining PRI in warm, calm days (cluster 2) within each species. Logliks (loglikelihood), K (number of parameters), w_i (Akaike weight value), ΔAIC (the model AIC value). If the model of best fit were a null model, the second model of best fit within that cluster was also given.

Species	Model of best fit	Logliks	K	w_i	ΔAIC
A. selago	Solar irradiance + VPD	-996.981	5	0.999	0
S. procumbus	Solar irradiance + Soil water	-914.307	4	0.736	0
A. magellanica	Wind speed + Solar irradiance + Relative humidity	-1237.426	5	1	0
A. stolonifera	Air temperature + Soil water	-70.898	4	0.480	0
R. lanuginosum	Wind speed + relative humidity	-1110.323	4	0.526	0
S. colerata	Wind speed + Air temperature + Soil water	-710.423	5	0.999	0

Cold, calm days

On cold, calm days, a combination of air temperature and VPD had the most significant effect in determining canopy temperatures of *A. selago*. The null model was selected as the model of

best fit for determining PRI measurements of *A. selago*. The second model of best fit was therefore also reported, showing that relative humidity had the highest influence on PRI measurements for *A. selago*.

The null model was selected as the model of best fit for determining canopy temperatures of *S. procumbus*. The second model of best fit was therefore also reported, showing that a combination of wind speed, air temperature and soil water had the highest influence on canopy temperatures for *S. procumbus*. The model of best fit influencing PRI measurements in *S. procumbus* on cold, calm days were soil water.

The null model was the model of best fit for determining canopy temperatures for *A. magellanica* on cold, calm days. The second model was therefore also reported, indicating that wind speed, air temperature and soil water had the highest significance for explaining canopy temperatures of *A. magellanica*. The null model was the model of best fit for determining PRI measurements for *A. magellanica* on cold, calm days. The second model was therefore also reported, indicating that wind speed and soil water had the highest influence in determining PRI measurements of *A. magellanica*.

The model of best fit influencing canopy temperatures of *A. stolonifera* was wind speed and VPD. The same model was the model of best fit influencing PRI measurements of *A. stolonifera*.

A combination of wind speed, air temperature and soil water had the highest influence on canopy temperatures of *R. lanuginosum*. Soil water had the highest influence in driving PRI measurements for *R. lanuginosum* on cold, calm days.

The null model was the model of best fit for determining canopy temperatures for *S. colerata* on calm days. The second model was therefore also reported, indicating that wind speed, air temperature and soil water had the highest significance for explaining canopy temperatures of *S. colerata* on cold, calm days. Soil water had the highest influence in driving PRI measurements for *S. colerata* on cold, calm days.

Table 5.14 GLM model section explaining canopy temperatures in cold, calm days (cluster 3) within each species. Logliks (loglikelihood), K (number of parameters), w_i (Akaike weight value), ΔAIC (the model AIC value). If the model of best fit were a null model, the second model of best fit within that cluster was also given.

Species	Model of best fit	Logliks	K	w_i	ΔAIC
A. selago	Air temperature + VPD	-150.534	5	1.068	0
S. procumbus	a) Null model	-1395.799	2	1	0
S. procumbus	b) Wind speed + Air temperature + Soil water	-951.083	5	<0.001	0
A. magellanica	a) Null model	-173.556	2	1	0
A. magellanica	b) Wind speed + Air temperature + Soil water	-125.705	5	<0.001	53.851
A. stolonifera	Wind speed + VPD	3779.295	5	0.733	0
R. lanuginosum	Wind speed + Air temperature +Relative humidity	82.724	5	0.995	0
S. colerata	a) Null model	-169.695	2	1	0
S. colerata	b) Wind speed + Air temperature + Soil water	-86.077	5	<0.001	89.617

Table 5.15 GLM model section explaining PRI in cold, calm days (cluster 3) within each species. Logliks (loglikelihood), K (number of parameters), w_i (Akaike weight value), ΔAIC (the model AIC value). If the model of best fit were a null model, the second model of best fit within that cluster was also given.

Species	Model of best fit	Logliks	K	w_i	ΔAIC
A. selago	a) Null model	-58.240	2	0.997	0
A. selago	b) Relative humidity	-46.268	3	0.001	13.792
S. procumbus	Soil water	-1399.26	3	0.675	0
A. magellanica	a) Null model	-173.556	2	1	0
A. magellanica	b) Wind speed + Soil water	-129.278	4	<0.001	0
A. stolonifera	Wind speed + VPD	-737.631	5	0.428	0
R. lanuginosum	Soil water	-6.284	3	1	0
S. colerata	Soil water	-188.279	3	0.999	0

Cold, cloudy days

The null model was the model of best fit for determining canopy temperatures for *A. selago* on cold, cloudy days. The second model was therefore also reported, indicating that wind speed, air temperature and VPD had the highest influence in determining canopy temperatures of *A. selago* on cold, cloudy days. The null model was the model of best fit for determining PRI measuremenys for *A. selago* on cold days. The second model was therefore also reported, indicating that soil water had the highest influence in determining canopy temperatures of *A. selago* on cold, cloudy days.

A combination of wind speed, air temperature and VPD had the highest significance for explaining canopy temperatures of *S. procumbus*. A combination of wind speed, air temperature and relative humidity had the highest influence on PRI measurements of *S. procumbus*.

The model of best fit for determining canopy temperatures for *A. magellanica* was wind speed, air temperature and relative humidity. A combination of wind speed and air temperature had the highest influence on PRI measurements of *A. magellanica.*

The null model was the model of best fit for determining canopy temperatures for *A. stolonifera* on cold, cloudy days. The second model was therefore also reported, indicating that wind speed and VPD had the highest influence in determining canopy temperatures of *A. stolonifera* on cold, cloudy days. The model of best fit influencing PRI measurements of *A. stolonifera* on cold, cloudy days was wind speed, solar irradiance and VPD.

The model for best fit influencing canopy temperatures of *R. lanuginosum* was solar irradiance and VPD. A combination of wind speed, solar irradiance and VPD had the highest influence on PRI measurements of *R. lanuginosum.*

A combination of wind speed, air temperature and relative humidity had the highest significance for explaining canopy temperatures of *S. colerata* on cold, cloudy days. The same combination of variables had the highest influence on PRI measurements than canopy temperature measurements for *S. colerata* on cold days.

Table 5.16 GLM model section explaining canopy temperatures in cold, cloudy days (cluster 4) within each species. Logliks (loglikelihood), K (number of parameters), w_i (Akaike weight value), ΔAIC (the model AIC value). If the model of best fit were a null model, the second model of best fit within that cluster was also given.

Species	Model of best fit	Logliks	K	w_i	ΔAIC
A. selago	a) Null model	-169.205	2	0.637	0
A. selago	b) Wind speed + Air temperature + VPD	-170.591	5	0.087	3.990
S. procumbus	Wind speed + Air temperature + Soil water	-1041.237	5	0.994	0
A. magellanica	Wind speed + Air temperature + relative humidity	-59.473	5	0.603	0
A. stolonifera	a) Null model	-428.147	2	1	0
A. stolonifera	b) Wind speed + VPD	4084.094	6	<0.001	53.129
R. lanuginosum	Solar irradiance + VPD	3124.265	5	0.943	0
S. colerata	Wind speed + Air temperature + relative humidity	-132.269	5	0.882	0

Table 5.17 GLM model section explaining PRI in cold, cloudy days (cluster 4) within each species. Logliks (loglikelihood), K (number of parameters), w_i (Akaike weight value), ΔAIC (the model AIC value). If the model of best fit were a null model, the second model of best fit within that cluster was also given.

Species	Model of best fit	Logliks	K	w_i	ΔAIC
A. selago	a) Null model	-169.205	2	0.148	0
A. selago	b) Soil water	-170.324	3	0.095	0.880
S. procumbus	Wind speed + Air temperature + Soil water	-1041.237	5	0.993	0
A. magellanica	Wind speed + Air temperature	-59.473	5	0.228	0
A. stolonifera	Wind speed + Solar irradiance + VPD	-375.174	4	0.994	0
R. lanuginosum	Wind speed + Solar irradiance + VPD	-64.324	4	0.639	0
S. colerata	Wind speed + Air temperature + relative humidity	-132.269	5	0.473	0

5.4.5. The relationship between environmental variables and vegetation indexes on a diurnal scale

Tables 5.18 – 5.21 give a general overview of the relationship between vegetation indexes (PRI and canopy temperatures) and environmental variables within each day archetype. The correlations were done on mean hourly values within each cluster to understand the diurnal relationship within each species. Only the environmental variables that were included in the GLM models of best fit influencing PRI and canopy temperatures will be discussed within each day archetype per species.

Warm, windy days

There was a significant negative correlation between canopy temperatures and PRI measurements, with PRI measurements decreasing (indicating stress) as canopy temperatures increase for *A. selago*. Looking at the variables in the model of best fit separately (as established in the GLM), it is clear that an increase solar irradiance has a negative impact on PRI measurements. One of the main drivers of PRI, based on the GLM, is soil water. An increase in soil water leads to a significant decrease in PRI values. There is a direct correlation between increase soil water and increases in VPD (Pearsons: $r = 0.607$, $p < 0.05$) (Table 5.18). The model of best fit influencing canopy temperatures of *A. selago* were the null model and correlations between environmental variables will not be mentioned specifically

There was a significant negative correlation between canopy temperatures and PRI measurements for *S. procumbus*. PRI measurements decreased with an increase in canopy temperatures. The model of best fit explaining PRI of *S. procumbus* was the null model and correlations between environmental variables will not be mentioned specifically

Looking at the variables separately of the model of best fit influencing canopy temperatures, we can see that an increase in wind speeds had a significant negative effect on canopy temperatures. Canopy temperatures were correlated with air temperatures, with an increase in air temperatures leading to an increase in canopy temperatures. Increases in soil water had a significant negative correlation with canopy temperatures.

There was no significant correlation between canopy temperatures and PRI measurements made for *A. magellanica*. The model of best fit influencing canopy temperatures of *A. magellanica* were the null model and correlations between environmental variables will not be mentioned specifically. The environmental variable influencing PRI measurements based on the GLM results are solar irradiance and soil water. While the combination solar irradiance and soil water together has a significant effect on PRI measurements on cold, calm days, there

is no significant correlation between PRI measurements and either one of these environmental variables.

There was a positive correlation between canopy temperatures and PRI measurements for *A. stolonifera*. The environmental variables affecting PRI measurements, based on the model of best fit for *A. stolonifera*, were air temperature and relative humidity. There was a significant negative relationship between relative humidity and PRI measurements, with PRI measurements decrease with an increase in relative humidity. There was a significant positive correlation between air temperature and PRI measurements, with PRI increasing as temperatures on cold, calm days. The canopy temperatures of *A. stolonifera* were significantly positively correlated with solar irradiance and VPD. Even though wind was one of the variables influencing canopy temperatures in *A. stolonifera* based on the model of best fit, wind on its own was not correlated with canopy temperatures on cold, calm days. This highlights the importance of different variables interacting with each other to control canopy temperatures.

PRI measurements of *R. lanuginosum* were significantly negatively correlated with canopy temperatures, with PRI measurements decreasing as canopy temperatures increase. The model of best fit influencing canopy temperatures of *R. lanuginosum* was the null model and correlations between environmental variables will not be mentioned specifically. Looking at the environmental variables separately influencing PRI measurements of *R. lanuginosum*, we can see that both air temperature and solar irradiance were negatively correlated with PRI measurements on cold, calm days.

PRI measurements of *S. colerata* were significantly negatively correlated with canopy temperatures, with PRI measurements decreasing as canopy temperatures increase. Canopy temperatures of *S. colerata* were significantly positively correlated to solar irradiance and VPD measurements on warm, wind days. PRI measurements of *S. colerata* were negatively correlated to solar irradiance and VPD measurements.

Table 5.18 Correlation between PRI and Canopy temperature and environmental variables in warm, windy days (cluster 1) across all species. Values represent Pearson correlation coefficient. (*= significant p-values) (T_{canopy} - canopy temperature, Solar – Solar irradiance, RH – Relative humidity, T_{air} – Air temperature, SVWC – Soil volumetric water content, T_{soil} – Soil temperature, kPa – Atmospheric pressure, wind – Wind speed, VPS – Vapour pressure deficit).

					A. selago					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.746***	**-0.766***	**0.793***	**-0.751***	**-0.552***	**-0.706***	0.323	**0.849***	**-0.566***
T_{canopy}	-	-	**0.989***	**-0.987***	**0.992***	**0.528***	**0.873***	0.158	**-0.927***	**0.853***
					S. procumbus					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.685***	**-0.627***	**0.719***	**-0.689***	-0.066	**-0.598***	**0.541***	0.102	-0.339
T_{canopy}	-	-	0.990	**-0.957***	**0.993***	0.437	**0.838***	-310	-0.325	**0.764***
					A. magellanica					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	0.221	0.193	-0.213	0.224	0.123	0.259	0.062	-0.356	0.09
T_{canopy}	-	-	**0.979***	**-0.959***	**0.990***	0.413	**0.955***	0.340	-0.268	**0.610***
					A. stolonifera					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**0.448***	0.398	**-0.476***	**0.471***	0.235	**0.424***	**-0.585***	0.071	0.129
T_{canopy}	-	-	**0.991***	**-0.866***	**0.997***	**0.602***	**0.906***	-0.295	-0.247	**0.797***
					R. lanuginosum					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.810***	**-0.807***	**0.879***	**-0.874***	0.127	**-0.719***	-0.038	**0.813***	**-0.571***
T_{canopy}	-	-	**0.972***	**-0.969***	**0.981***	-0.056	**0.857***	0.156	**-0.743***	**0.722***
					S. colerata					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.918***	**-0.901***	**0.871***	-0.931	-0.364	**-0.886***	**0.543***	0.211	**-0.609***
T_{canopy}	-	-	**0.989***	**-0.903***	**0.993***	0.245	**0.988***	-0.304	-0.308	**0.780***

Warm, calm days

There was a significant negative correlation between canopy temperatures and PRI measurements of *A. selago* in warm, calm days. Canopy temperatures of *A. selago* were significantly positively correlated with VPD. Looking at solar irradiance separately we can see that without the interaction with VPD, there is no correlation between canopy temperatures and solar irradiance. The inverse can be seen in PRI measurements of *A. selago*, with PRI measurements being significantly negatively correlated to solar irradiance. There is no correlation seen between VPD and PRI measurements in warm, calm days (Table 5.19).

There was no significant correlation between canopy temperatures and PRI measurements of *S. procumbus* made on warm, calm days. There was no correlation between wind speeds and canopy temperatures seen for *S. procumbus*. There was a significant positive correlation seen between air temperature and canopy temperature, with canopy temperatures increasing as air temperatures increasing. There was no significant correlation between PRI measurements for *S. procumbus* and solar irradiance and soil water respectfully, even though these variables interaction had the highest effect ion PRI measurements base on the GLM.

There was no correlation between canopy temperature and PRI measurements made for *A. magellanica* on warm, windy days. Based on the GLM, wind, air temperatures, and soil water had the most effect on canopy temperatures measured. Looking at these variables separately we can see that air temperature and soil water has a significant positive correlation with canopy temperatures measured, while increase wind speeds has a significant negative effect on canopy temperatures, with canopy temperatures of *A. magellanica* decreasing with increased wind speeds. There was no correlation between individual environmental variables and PRI measurements made for *A. magellanica*.

There was no relationship between canopy temperatures and PRI measurements made for *A. stolonifera* on warm, calm days. Based on the variables selected by the model of best fit, there is a significant positive correlation between canopy temperatures and air temperatures. There is significant negative correlation between canopy temperatures and wind speeds as well as relative humidity for *A. stolonifera*. There was no correlation between individual environmental variables and PRI measurements made for *A. stolonifera* (Table 5.19).

There was a significant negative correlation between canopy temperatures and PRI measurements made for *R. lanuginosum* on warm, calm days. There was a significant positive correlation between air temperature and canopy temperatures, with canopy temperatures increasing as air temperatures increase. There was a significant negative correlation between

canopy temperatures and wind with no correlation to soil water. There was a significant positive correlation between PRI measurements made and wind speeds on warm, calm days. There was a significant positive correlation between PRI measurements made for *R. lanuginosum* and relative humidity (Table 5.19).

There was a significant negative correlation between canopy temperatures and PRI measurements made of *S. colerata* on warm, calm days. Canopy temperatures had no significant correlation with soil water and wind speeds. PRI measurements of *S. colerata* had no correlation with wind. There was a significant negative correlation between PRI measurements made and air temperatures, with PRI decreasing as air temperatures increase. PRI measurements of *S. colerata* were not significantly correlated to soil water (Table 5.19).

Table 5.19 Correlation between PRI and Canopy temperature and environmental variables in warm, calm days (cluster 2) across all species. Values represent Pearson correlation coefficient. (* = significant p-values) (T_{canopy} - canopy temperature, Solar – Solar irradiance, RH – Relative humidity, T_{air} – Air temperature, SVWC – Soil volumetric water content, T_{soil} – Soil temperature, kPa – Atmospheric pressure, wind – Wind speed, VPS – Vapour pressure deficit).

					A. selago					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.601***	**-0.552***	**0.686***	**-0.591***	-0.108	**-0.588***	-0.348	**0.771***	-0.392
T_{canopy}	-	-	0.993	**-0.969***	**0.993***	0.356	**0.935***	**0.405***	**-0.61***	**0.909***
					S. procumbus					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	-0.165	-0.114	0.038	-0.113	-0.119	-0.162	0.161	**-0.096***	-0.138
T_{canopy}	-	-	0.930	**-0.840***	**0.963***	0.649	**0.969***	-0.249	-0.038	**0.839***
					A. magellanica					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	0.244	0.204	-0.334	0.243	0.130	0.193	0.152	-0.558	0.089
T_{canopy}	-	-	**0.996***	**-0.962***	**0.996***	**0.789***	**0.981***	0.349	**-0.744***	**0.912***
					A. stolonifera					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	0.018	0.015	-0.126	0.055	-0.099	0.056	0.118	-0.192	-0.068
T_{canopy}	-	-	**0.994***	**-0.973***	**0.983***	**0.582***	**0.906***	0.199	**-0.415***	**0.907***
					R. lanuginosum					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.753***	**-0.749***	**0.799***	**-0.793***	0.061	**-0.688***	0.039	**0.770***	**-0.594***
T_{canopy}	-	-	**0.997***	**-0.952***	**0.991***	-0.025	**0.866***	0.066	**-0.618***	**0.907***
					S. colerata					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.893***	**0.907***	**0.949***	**-0.935***	-0.128	**-0.858***	-0.176	0.539	**-0.820***
T_{canopy}	-	-	**0.991***	**-0.974***	**0.979***	0.078	**0.991***	0.167	-0.335	**0.898***

Cold, calm days

There was a strong negative correlation between PRI measurements and canopy temperatures for *A. selago* on cold, calm days, with PRI measurements decreasing as canopy temperatures increase. There was a significant positive correlation between canopy temperatures and both VPD and air temperature. The null model was the model of best fit influencing PRI measurements of *A. selago* on cold, calm days (Table 5.20).

There was a significant positive correlation between canopy temperature and PRI measurements for *S. procumbus* on cold, calm days. The null model was the model of best fit influencing canopy temperatures on cold, calm days and correlations to environmental variables are therefore not mentioned. PRI measurements for *S. procumbus* had no significant correlation with soil water (Table 5.20).

There was no correlation between canopy temperatures and PRI measurements made for *A. magellanica* on cold, calm days. The null model was the model of best fit influencing both canopy temperatures and PRI measurements made for *A. magellanica* on cold, calm days and correlations to environmental variables are therefore not mentioned.

There was no significant correlation between canopy temperatures and PRI measurements made for *A. stolonifera* on cold, calm days. Canopy temperatures were significantly positively correlated to wind and VPD respectively. PRI measurements for *A. stolonifera* were not significantly correlated to either wind or VPD, even though those variables were included in the model of best fit influencing PRI measurements (Table 5.20).

There was a significant negative correlation between canopy temperatures and PRI measurements made for *R. lanuginosum* on cold, calm days, with PRI measurements decreasing as canopy temperatures increase. Canopy temperatures of *R. lanuginosum* were significantly negatively correlated to wind speeds, with canopy temperatures decreasing as wind speeds increase. Canopy temperatures were significantly positively correlated to air temperature and negatively correlated to relative humidity. PRI measurements made for *R. lanuginosum* was not significantly correlated to soil water on cold, calm days.

There was a significant correlation between PRI measurements and canopy temperatures made for *S. colerate* on cold, calm days. The null model was the model of best fit influencing canopy temperatures for *S. colerata*, and correlations between environmental variables will not be mentioned specifically. PRI measurements made for *S. colerata* were not significantly correlated to soil water on cold, calm days.

Table 5.20 Correlation between PRI and Canopy temperature and environmental variables in cold, calm days (cluster 3) across all species. Values represent Pearson correlation coefficient. (* = significant p-values) (T_{canopy} - canopy temperature, Solar – Solar irradiance, RH – Relative humidity, T_{air} – Air temperature, SVWC – Soil volumetric water content, T_{soil} – Soil temperature, kPa – Atmospheric pressure, wind – Wind speed, VPS – Vapour pressure deficit).

					A. selago					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.629***	**-0.533***	**0.563***	**-0.607***	0.371	**-0.647***	**-0.480***	**-0.671***	**-0.474***
T_{canopy}	-	-	**0.945***	**-0.909***	**0.991***	0.011	**0.955***	**0.509***	**0.906***	**0.841***
					S. procumbus					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**0.409***	**0.512***	**-0.566***	**0.561***	0.139	0.371	0.179	0.180	0.397
T_{canopy}	-	-	**0.909***	**-0.869***	**0.936***	0.121	**0.972***	0.542	0.316	**0.886***
					A. magellanica					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	-0.063	-0.067	-0.106	-0.079	-0.236	-0.034	0.067	-0.014	-0.128
T_{canopy}	-	-	**0.929***	**-0.905***	**0.985***	**0.685***	**0.985***	0.525	**0.879***	**0.825***
					A. stolonifera					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	0.294	0.363	**-0.482***	0.379	-0.161	0.305	0.370	0.278	0.185
T_{canopy}	-	-	**0.914***	**-0.909***	**0.963***	**0.462***	**0.974***	**0.573***	**0.536***	**0.906***
					R. lanuginosum					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.685***	**-0.795***	**0.868***	**-0.749***	-0.089	-0.394	-0.261	**-0.463***	**-0.665***
T_{canopy}	-	-	**0.949***	**-0.893***	**0.987***	**0.662***	**0.831***	**0.476***	**0.854***	**0.844***
					S. colerata					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.740***	**-0.836***	**0.869***	**-0.822***	0.028	**-0.688***	-0.202	-0.404	**-0.725***
T_{canopy}	-	-	**0.938***	**-0.938***	**0.974***	**0.439***	**0.989***	**0.478***	**0.672***	**0.944***

Cold, cloudy days

There was no significant correlation between canopy temperature and PRI measurements made for *A. selago* on cold days. The null model was the model of best fit influencing canopy temperatures for *A. selago*, and correlations between environmental variables will not be mentioned specifically. The null model was the model of best fit influencing PRI measurements for *A. selago*, and correlations between environmental variables will not be mentioned specifically.

There was no significant correlation between canopy temperature and PRI measurements made for *S. procumbus* on cold days. Canopy temperatures were significantly positively correlated to air temperatures, with canopy temperatures increasing as air temperatures increased on cold days. There was a significant positive correlation between canopy temperatures made for *S. procumbus* and wind. PRI measurements made *for S. procumbus* was not significantly correlated to individual environmental variables (Table 5.21).

There was no significant correlation between canopy temperature and PRI measurements made for *A. magellanica* on cold days. Canopy temperatures were significantly correlated with both wind as well as air temperature. Canopy temperatures of *A. magellanica* were significantly correlated to relative humidity on cold days. PRI measurements made for *A. magellanica* was not significantly correlated to individual environmental variables

There was a significant positive correlation between canopy temperatures and PRI measurements made for *A. stolonifera*, with PRI measurements increasing as canopy temperatures increase on cold days. The null model was the model of best fit influencing canopy temperatures for *A. stolonifera*, and correlations between environmental variables will not be mentioned specifically. PRI measurements were significantly correlated with wind, VPD as well as solar irradiance on cold days (Table 5.21).

There was a significant negative correlation between canopy temperatures and PRI measurements made for *R. lanuginosum* on cold days, with PRI measurements decreasing as canopy temperatures increase. Canopy temperatures have a significantly positive correlation with both solar irradiance and VPD. There was a significant negative correlation between PRI measurements made for *R. lanuginosum* and solar irradiance. PRI measurements are also significantly negatively correlated to both wind and VPD on cold days (Table 5.21).

There was a significant negative correlation between canopy temperatures and PRI measurements made for *S. colerata* on cold days, with PRI measurements decreasing as canopy temperatures increases. There is a significant positive correlation between canopy

temperatures and both air temperature and wind. There is a significant negative correlation between relative humidity and canopy temperatures for *S. colerata* on cold days. The inverse correlations can be seen in PRI measurements, with PRI measurements being significantly negatively correlated with wind and air temperature, and significantly positively correlated with relative humidity on cold days (Table 5.21).

Table 5.21 Correlation between PRI and Canopy temperature and environmental variables in cold, cloudy days (cluster 4) across all species. Values represent Pearson correlation coefficient. (* = significant p-values) (T_{canopy} - canopy temperature, Solar – Solar irradiance, RH – Relative humidity, T_{air} – Air temperature, SVWC - Soil volumetric water content, T_{soil} – Soil temperature, kPa – Atmospheric pressure, wind – Wind speed, VPS – Vapour pressure deficit).

					A. selago					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	-0.388	-0.260	0.174	-0.392	-0.332	-0.353	0.397	-0.327	-0.229
T_{canopy}	-	-	**0.975***	**-0.837***	**0.993***	**0.835***	**0.947***	-0.400	**0.578***	**0.901***
					S. procumbus					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	-0.512	-0.377	0.266	-0.545	-0.351	-0.516	0.456	-0.346	-0.399
T_{canopy}	-	-	**0.976***	**-0.740***	**0.993***	0.528	0.921*	-0.490	**0.662***	**0.938***
					A. magellanica					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	0.242	-0.086	-0.072	0.297	0.172	0.036	0.075	0.310	0.211
T_{canopy}	-	-	**0.819***	**-0.859***	**0.983***	**0.814***	**0.900***	**-0.574***	**0.709***	**0.818***
					A. stolonifera					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**0.602***	**0.504***	-0.399	**0.618***	0.207	**0.520***	-0.247	**0.512***	**0.557***
T_{canopy}	-	-	**0.953***	**-0.719***	**0.999***	0.543	**0.971***	-0.525	**0.758***	**0.930***
					R. lanuginosum					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.882***	**-0.821***	**0.552***	**-0.879***	0.231	**-0.804***	**0.426***	**-0.601***	**-0.719***
T_{canopy}	-	-	**0.966***	**-0.689***	**0.985***	-0.147	**0.878***	-0.348	**0.582***	**0.879***
					S. colerata					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.937***	**-0.896***	**0.717***	**-0.938***	**-0.436***	**-0.891***	0.363	**-0.690***	**-0.869***
T_{canopy}	-	-	0.948	**-0.736***	**0.996***	**0.569***	**0.977***	**-0.474***	**0.78***	**0.931***

5.5. Discussion

5.5.1. Diurnal response of PRI

Solar irradiance is temporally very heterogeneous especially on a diurnal scale due to cloud movement experienced on the Marion Island. Days with high solar irradiance can be experienced as well as days with low solar irradiance, or a mixture of both. Plants with high photosynthetic rates do not utilize more than half of the solar energy absorbed during peak solar irradiance. This can be significantly less in species with lower photosynthetic rates (Demmig-Adams and Adams, 1996). Under high solar irradiance, more than 50% of the incoming energy can be dissipated depending on the capability of plants to convert this energy photo-chemically (Valladares, 2003). The amount ofenergy dissipated can increase by up to 90% due to the influence of a stress factor on the plant (Valladares, 2003; Demmig-Adams and Adams, 2006). Different physiological plasticity can be seen in plants acclimated to different light levels. Plants adapted to low light environments might experience significant stress in high light environments (Demmig-Adams and Adams, 2006).

Most plants, however, are tolerant to changing light environments, showing physiological plasticity in response to solar irradiance variability. Photosynthetic activity will accelerate in response to increases in light levels not exceeding the plant's capacity to convert solar energy photo-chemically. This response might be slow at first, if plants have been acclimated to a shade (low light) environment. Induction rates can often require 10-30 minutes, during which plants can experience stress due to the increased solar irradiance (Valladares, 2003) Once leaves are fully induced, they can recover quickly to optimal photosynthesis after being exposed to a shaded (low light) environment for short periods of time (Valladares, 2003). This is important for optimising incoming solar energy in a highly variable light environment, such as Marion Island where cloud movements influence the light environment.

A midday depression can be seen in PRI measurements in all plants at peak solar irradiance. However in the cushion plants this can only be seen in days with average high solar irradiance levels. On days with low solar irradiance levels, the PRI measurements of cushion plants mimics the solar irradiance patterns, experiencing less stress with increased midday solar irradiance levels on low solar days. Marion Island is known as a low light environment due to the presence of clouds. Maximising the use of low levels of incoming solar irradiance is important to maximise photosynthetic activity under low light environments. Due to an almost constant presence of clouds, Marion Island only receives 20-30% of the possible maximum solar input at this latitude (Smith and Steenkamp, 1990). It has been shown that plants in the sub-Antarctic still uses incoming solar energy as effectively under low light levels as plants in the Northern tundra systems (Smith, 1987c).

The midday PRI decreases seen across species, coincides with peak temperatures measured during the day (Demmig-Adams and Adams, 1996). Significant stress can be experienced during high temperatures when temperatures exceed optimums depending on species and growing conditions. For cushion plants, and *A. selago* specifically, a significant negative relationship has been seen on Marion Island under warming conditions in regards with growth and production (le Roux *et al.* 2005). Reduced light under these stress conditions can therefore be positive for this species (le Roux *et al.* 2005). Inspection of diurnal response of stress shows that the deepest depression in PRI for both cushion plants coincides with high solar irradiance and increased temperatures. In cold temperatures, the positive affect of low solar irradiance levels was seen, with less stress experienced for both cushion plants.

Even though an increase in stress can be seen at midday levels for both grass species across all day archetypes, higher PRI measurements were seen in warmer days (with a decreased midday depression). A broad optimum temperature range has been shown for both *Agrostis* species on Marion Island (Pammenter *et al.* 1986). The optimum temperature ranges for these grasses have been shown to range from 10 to 20°C (Pammenter *et al.* 1986). Increased photosynthetic performance with decreased stress can therefore be expected during average warmer days.

Plants that are adapted to low light environments can experience significant stress during increased light levels and temperatures (Valladares, 2003). In lower plants this is often seen where these plants are dried under high temperatures and increased light levels. This is due to the lack of water conducting elements in lower plants (Russell, 1990, Valladares, 2003). There is a strong correlation between lower plant production and moisture (Russell, 1990). The deepest depression in PRI measurements in lower plants were seen in warm days with high solar irradiance levels compared to cold days with low light levels.

Increased wind speeds can lead to increased water loss in species as well as decreased canopy temperatures (French and Smith, 1985). The effect of wind on canopy temperatures can be seen, where there was no difference in canopy temperatures measured between warm days with high wind speeds and cold days with low wind speeds. Only the canopy temperatures of grasses seem not to be significantly decreased by high wind speeds, since canopy temperatures for both grasses were still significantly different between warm days with high wind speeds and cold days with low wind speeds. This highlights how canopy structure influences temperatures within a canopy. VPD measurements on the different type of days are low due to the high humidity levels experienced on Marion Island (French and Smith, 1985). From visual inspection the deepest PRI depression coincides with the peak air temperatures and VPD (Demmig-Adams and Adams, 1996).

5.5.2. Relationship between vegetation indices and environmental variables

When inspecting PRI measurements, a large decrease in the PRI signal in response to changing environmental conditions should indicate de-epoxidation of the xanthophyll cycle and therefore limit photosynthesis (Magney *et al.* 2016). A stressful environment should lead to the decrease in photosynthesis and production (Magney *et al.* 2016). There was significant diversity in PRI responses in relation to environmental variables seen between different functional groups.

On warm, windy days PRI measurements were negatively affected by increased canopy temperatures in both cushion plants and lower plants species. Correlations between PRI measurements and canopy temperatures for both grasses are rarely seen, highlighting the importance of growth form affecting plant physiology. Significant differences between gas exchange and photosynthesis have been recorded for C_3 plants with different growth forms (Franks and Farquhar, 1999). For all plants where a decrease in PRI measurements were seen as canopy temperatures increased, the same negative relationship between PRI measurements and air temperatures were seen. This response was seen across all days, besides cold days, where air temperatures and canopy temperatures on average were ±5°C.

With an increase in both air temperatures and canopy temperatures, cushion plants experienced significantly more stress. Increased temperatures that exceeds the photosynthetic optimum of plant species, can lead to a decrease in photosynthetic rates. This can have negative effects on carbon assimilation (production) in plants (Sharkey, 2005). Temperature increases (either canopy-, soil- or air temperature increases), had positive effects on PRI measurements of grasses. Both *A. magellanica* and *A. stolonifera* have large temperature ranges for optimal photosynthesis. Optimum temperature ranges for *Agrostis* species on Marion Island are between 10 and 20°C, which are lower than mean annual temperatures experienced. A significant decrease in photosynthesis can be seen in temperatures below the optimum where the grass species are experiencing stress (Pammenter *et al.* 1986). The positive effect of increased temperatures are therefore seen in both grasses especially on cold days.

Lower plant production is highly influenced by moisture in the surrounding habitat (Russell, 1990). This can be seen in the positive relationship between relative humidity and PRI measurements in lower plant species across all days. Since there was relative little fluctuation in soil water throughout the study period at the study sites, there was no significant correlations seen between PRI measurements and soil water measurements. Photosynthetic rates of lower plant species at coastal sites in Point Barrow, was found not to be limited by soil water but rather temperature and light (Longton, 1988). Since lower plant species are influenced by habitat moisture regimes,

increased temperatures can lead to increased stress. Increased temperatures can lead to increased rates of desiccation in lower plant species (Russell, 1990).

Wind has been thought to suppress stomatal conductance, since plants would need to avoid decreasing transpiration and temperatures to avoid freezing due to the chill factor (Smith and Steenkamp, 2001), however wind can also have a positive effect by decreasing temperatures in warmer microclimates (Smith and Steenkamp, 1990; Rouault, 2005). When stress is experienced due to increased temperatures, the effect of wind can play a major role in reducing temperatures. In cushion plants significant stress is experienced due to increased temperatures, especially on hot days. The positive effect of wind controlling temperatures can be seen on warm, windy days for cushion plants. Wind decreases canopy temperatures for cushion plants and is therefore positively correlated to PRI measurements on hot days. This effect can also be seen in lower plant species, however the positive effect of increased wind speeds is limited in lower plant since increased wind speeds can lead to increased water loss (Russell, 1990).

The effect of increased wind speeds is highly variable for both grass species across the different types of days. Increased wind speeds can lead to mechanical damage in grass species. High wind speeds can therefore have a negative effect on the *Agrostis* species (Ennos, 1997). Increased wind speeds were negatively correlated to PRI measurements of both grasses, however only on days with high wind speeds. This can be a result of damage due to wind speeds or the decrease of temperatures within the canopy due to increased wind speeds. Both grass species have high temperature optima for photosynthesis (higher than annual average on Marion Island) (Pammenter *et al.* 1986). Decreasing temperatures within the canopy can have a significant negative effect in photosynthesis and production of grasses.

Plants balance maximum carbon uptake while decreasing water loss. Fluctuations in daily VPD can lead to changes in water loss rates due to transpiration (Franks and Farquhar, 1999). Marion Island has annual high levels of relative humidity and in effect VPD ranges are small (Bergstrom and Chown, 1999). Plants decrease water loss at increasing VPD through means of stomatal control (Franks and Farquhar, 1999). In lower plant species where there is a lack of water conducting elements, the negative effect of increased VPD can be clearly seen (Russell, 1990; Valladares, 2003). PRI measurements of lower plant species was negatively correlated to increases to VPD across all days. Lower plants species are highly influenced by moisture, and VPD increases can lead to a loss in moisture due to transpiration (Russell, 1990; Franks and Farquhar, 1999). In higher plant species, increased VPD is not significantly correlated with increased stress since higher plant species can minimize water loss (especially in low VPD measurements) by means of stomatal control. The only higher plant species being negatively affected by increased VPD levels, was

A. selago. In plants with higher transpiration rates a decrease in leaf water potential due to increasing VPD is often seen. This effect has been shown to increase in woody plants, and can have negative effects on photosynthesis and production (Franks and Farquhar, 1999; Turner, *et al.* 2017).

5.5.3. Environmental drivers of diurnal physiological patterns

The effect of environmental variables as drivers cannot be determined by inspecting single variables alone. Interactions between multiple environmental variables can have a range of different effects, with changes in environmental variables not only affecting PRI measurements, but also affecting each other. Predictions made based on single environmental drivers can therefore be misleading and deceptive when the interactive effects between variables are ignored (le Roux *et al.* 2005). To understand the environmental drivers of stress and photosynthesis, a multi-parameter approach needs to be taken.

The importance of moisture regimes as a driver for both *A. selago* and *S. procumbus* on a diurnal scale is evident in the driver model selection across all days. Changes in moisture regimes (soil water, relative humidity or VPD) were one of the main drivers of stress across all day archetypes for *A. selago* and *S. procumbus*. The combination of increased solar irradiance and changes in soil water had significant effects on driving diurnal PRI patterns. A decrease in a plants ability to convert incoming energy photo-chemically decreases drastically under the influence of a stress factor (Demmig-Adams and Adams, 1996). Decreases in habitat moisture can lead to increases in water loss and a balance between optimum carbon uptake through photosynthesis while minimising water loss needs to be found (Franks and Farquhar, 1999). Loss in water due to increased transpiration rates as a result of increased VPD can be minimised by stomatal control. It has been shown that in woody plant species, the water potential of a leaf decreases with increased VPD indicating efficient water conducting elements (Franks and Farquhar, 1999; Turner *et al.* 2017). Increased solar irradiance coupled with increase temperatures during midday can lead to drying of the surrounding habitat (Valladares, 2003). At peak solar irradiance levels during the day (midday), higher levels of stress are experienced by *A. selago* and *S. procumbus* leading to the need to increase the dissipation of incoming energy (Demmig-Adams and Adams, 1996; Valladares, 2003).

The combination of wind speed, air temperatures and habitat moisture (soil water, relative humidity or VPD) changes were the main drivers for *A. magellanica* across all days. *A. magellanica* has a wide temperature optimum range for photosynthesis (Pammenter *et al.* 1986) and temperature dependant photo-inhibition has been recorded for *A. magellanica.* Reductions in photosynthesis can be up to 20–35% when temperatures go below the optimum ranges (Pammenter *et al.* 1986). Temperature increases are therefore positively correlated to PRI measurements; however wind speeds can drastically decrease temperatures within the canopy. The combination of wind speeds

and air temperature significantly influence stress within *A. magellanica*, with these two variables having an antagonistic influence on diurnal PRI patterns. Increased wind speeds can also lead to an increase in water loss. On days with high incoming solar energy, solar irradiance together with moisture patterns was one of the main drivers for diurnal PRI patterns. With high temperatures and solar irradiance levels a decrease in habitat moisture can be found with increased VPD measurements. Herbaceous plants often display low water use efficiencies, with high productivity, and photosynthesis being coupled with increased water loss (Franks and Farquhar, 1999). During periods of decreased habitat moisture, decreases in photosynthesis and production are often seen.

Higher rates of carbon assimilation in response to increases in solar irradiance have been documented for *A. stolonifera* compared to *A. magellanica*. However carbon assimilation in *A. magellanica* increased significantly with increased temperatures (Pammenter *et al.* 1986). The importance of temperature in driving PRI patterns for *A. magellanica* is therefore strongly supported in this study.

Moisture (soil water, relative humidity or VPD) regimes are one of the main drivers for PRI patterns on a diurnal scale for *A. stolonifera*. *A. stolonifera* has the potential for high rates of transpiration. Changes in habitat moisture regimes therefore can have a significant effect on PRI patterns during the day when evaporation might be higher (Pammenter *et al.* 1986). On warm days increases in air temperature can decrease habitat moisture, therefore creating a stress environment for *A. stolonifera*. This interaction between temperature and moisture can be seen on warm days, therefore being the main drivers of diurnal PRI patterns.

On days with low air temperatures, the importance of moisture loss in *A. stolonifera* is apparent. Increased wind speeds can lead to an increase in water loss. The combination of increased VPD and wind speeds therefore can decrease photosynthesis in *A. stolonifera* by influencing moisture loss within the plant (Pammenter *et al.* 1986; Franks and Farquer, 1999). *A. stolonifera* has shown to have higher carbon assimilation rates at low photosynthetic photon flux density (PPFD) levels compared with *A. magellanica* (Pammenter *et al.* 1986). Solar irradiance levels play an important role in driving diurnal PRI patterns of *A. stolonifera* on days with low incoming solar irradiance levels.

In lower plant species, habitat moisture as well as exposure have significant influences on production and photosynthetic rated (Russell, 1990). Lower plant species are susceptible to desiccation, since they lack well-developed water conduction elements (Russell, 1990; Valladares, 2003). The main drivers for diurnal PRI patterns in lower plant species are therefore variables effecting moisture regimes and increased plant desiccation. *R. lanuginosum* has low rates of

productivity and increases in water loss can be significant in decreasing production (Russell, 1990). On warm days increased solar irradiance and increased air temperatures can lead to increased desiccation rates within *R. lanuginosum*. On cold days with low solar irradiance levels, other variables that can lead to increases in water loss are the main drivers of diurnal PRI patterns. These variables include a combination of increased wind speeds as well as changes in habitat moisture regimes (soil water, RH or VPD). The same diurnal drivers can be seen for *S. collerata* as those for for *R. lanuginosum*. Strong correlations between stress and habitat moisture levels in lower plant species have been recorded at other sub-Antarctic island and these studies show the importance of moisture regimes on a diurnal scale for both *R. lanuginosum* and *S. collerata* (Russell, 1990)..

5.6. Conclusions

Diurnal drivers of stress can vary significantly between different functional groups. General assumptions can therefore not be made about what drives diurnal stress patterns across different PFTs and species, since a clear difference in response to environmental variables can be seen. Environmental variability on a small time scale can have a significant effect on photosynthetic rates of plants, especially since plasticity in physiological response to different environmental variables varies between different plant functional types and species. A midday PRI depression was seen for all species, except for *A. selago* and *S. procumbus* where this pattern was not seen on cold and warm, calm days. The diurnal PRI patterns seemed to follow the expected diurnal PRI pattern where the deepest depression occurring at the highest air temperature and VPD measurements. The exception to this was *A. selago* and *S. procumbus*. Wind as a diurnal driver was highlighted with wind having both a positive and negative role, by either decreasing canopy temperatures on warm days that exceeded temperature optima of plants or increasing water loss in lower plant species. The importance of variability in the physiological response between different plant functional types was also highlighted, with segregation in PRI response seen between different functional groups.

6. Physiological responses of key plant functional types on a Sub-Antarctic Island in response to seasonal environmental change

6.1. Abstract

Production rates on Marion Island are well below the estimated rates and the proposed long growing season. Focus in this chapter is therefore given to determine what the seasonal stress and physiological responses are of different plant functional types. During the study there was a clear shift in climate during the "winter" and "summer" months, with warmer, windier days being experienced in the latter. This was mimicked in the growing degree day model, where an increase in temperatures exceeding baseline temperatures was seen during the "summer" months. The seasonal response of different functional groups was seen, with distinct stress patterns seen between different functional groups. Even with seasonal trends being similar within functional groups, variability was still seen between species of the same functional type. This showed that there are different environmental drivers for different species, but overlap in these drivers can be seen within species of the same functional group.

6.2. Introduction

Very little is known about the in-field physiological behaviour of sub-Antarctic species. The annual production on Marion Island is well below the possible potential based on NPP models (Lieth, 1973). Different communities deviate in distinct ways from predicted production values (Smith 1987a, b, c, d). This chapter will explore the seasonal and physiological performance of key functional types (cushion plants, graminoids, lower plants) in order to shed light on why this is the case, and what the possible role of main environmental drivers in this relationship is.

The PRI signal is a measure of photo-protective mechanism (the xanthophyll cycle). It tracks changes in photosynthetic efficiency over small time scales (Gamon *et al.* 1992; Gamon 2011; Gamon *et al.* 2015). Photosynthetic efficiency is very likely to be an important predictor of plant production, and therefore monitoring diurnal and seasonal patterns in this measure are useful for developing an initial understanding of the limitations to production of key plant functional types.

Drivers of seasonal stress can vary highly between different functional groups. Different environmental variables have been proposed as some of the main drivers of production on Marion Island including solar irradiance levels and wind speeds, however this has not been fully explored yet (Smith 1987d; Smith and Steenkamp, 2001). By understanding how seasonal changes in environmental variables affect stress on Marion Island, we can get an understanding on what drives production and photosynthetic efficiency throughout the growing season.

The growing season has been proposed to be between middle August until middle of June (Smith, 1987d). This has been proposed to be due to the stable temperature ranges through the seasons, however high variability in temperature have been seen during our study period. By looking at drivers of environmental stress on Marion Island we can get an understanding of whether the growing season is as long as proposed.

On a seasonal scale there can often be discrepancies when interpreting the seasonal component of the PRI signal (Stylinski *et al.* 2002; Gamon *et al.* 2015). Over multiple seasons, the PRI signal is not just influenced by changes in the xanthophyll pigments, but also influenced by other carotenoid changes (such as chlorophyll ratios) (Gamon *et al.* 2015). This is also likely to be true of different functional types. Different strategies are used by plants in order to dissipate excessive light energy on both diurnal scales and seasonal scales. This can be either through changes in the xanthophyll pigments (over short timescales) or changes in other carotenoid pigments such as chlorophyll pigment ratios (over seasonal scales) (Filella *et al.* 2009). Various studies have focussed on the diurnal component of the PRI signal when tracking physiological changes, however this is often not a true reflection of the changes seen over multiple growing season (Gamon *et al.* 1997; Stylinski *et al.* 2002; Gamon *et al.* 2015). It is therefore important to understand the effect of carotenoids (besides xanthophyll pigments) in order to interpret the seasonal component of the PRI signal.

This chapter will explore what drives patterns of physiological stress and photosynthetic performance on a seasonal scale, and whether these patterns are different for different functional groups. This will be done by identifying seasonal trends of physiological stress and photosynthetic performance and testing for relationships between these trends and changes in the main biophysical drivers for different functional groups.

6.3. Data analysis

6.3.1. Seasonal trends

The proportion of four diurnal archetypes (as defined in the previous chapter) within each month was calculated in order to determine if there was a seasonal change in climatic conditions. The number of growing degree days (GDD) was determined throughout the year. Since there is no literature available about the baseline temperatures for metabolic process for the species on Marion Island, the GDD was determined for three different base line temperatures, namely 0, 5 and 10°C. If the average temperature was below the base line temperature, the temperature was then set to equal the base line temperature (McMaster and Wilhem, 1997).

The number of water stress days were calculated for each month by determining the number of days per month where the average daily soil water dropped below a certain threshold, namely 0.1, 0.15 and 0.2 $m^3.m^3$.

The maximum xanthophyll inter-conversion occurs at peak solar irradiance levels, with maximum temperatures and VPD (Demmig-Adams and Adams. 1996; Magney *et al.* 2016). Due to the variability of climate seen on Marion Island, especially on a diurnal scale, specific time points during the day cannot be selected to track PRI trends throughout the seasons. To account for the variability in diurnal climate (and therefore PRI), daily average PRI measurements were used to determine seasonal changes and trends.

To determine if there was a positive or negative trend behaviour in PRI measurements, the seasonal component of the dataset was modelled. The annual cycle was scaled to be the length of 1.0 (1.0 = 365 days). A loess curve was applied on the average daily PRI measurement over time for each species.

6.3.2. Seasonal relationship between vegetation indexes and environmental variables

To determine if there is any relationship between the vegetation indexes (PRI and canopy temperature), a Pearson correlation was used. The correlation was performed between the vegetation indexes and all other environmental variables using the average daily values throughout the seasons.

A generalised additive model (GAM) with Gaussian distribution was used to determine seasonal drivers of different environmental variables (or combination of variables) for both PRI and canopy temperature measured for all species. The fixed effects variables were, air temperature, soil temperature, solar irradiance, VPD, atmospheric pressure, relative humidity wind speed and soil water. Collinearity between all variables were tested for and excluded from the analysis as fixed effects if collinearity was found.

A second order Akaike's Information Criterion (AIC) was then applied to determine which variables (or combinations) had the highest influence in PRI and canopy temperatures for each species. Maximised log likelihoods, model weights and AIC differences were calculated for each model. A null model for both PRI and canopy temperature was included in the mixed models to determine if the variation seen in both canopy temperature and PRI measured are a reflection of changes in environmental variables and not due to an unmeasured variable. This was done independently for all species.

6.4.Results

6.4.1. Seasonal environmental conditions

Changes in the frequency of types of days (as defined in the previous chapter) can be seen between the "winter" and "summer" months on Marion Island (Figure 6.1). An increase in warm, windy days can be seen in December, January and February with cold, calm days not seen during these months. A higher percentage of cold, calm days and cold, cloudy days can be seen in May until September (the winter months on Marion Island) (Figure 6.1). There is an abrupt seasonal shift in November and December from cold, calm days to warm and windy days. This shift can be seen to be reversed during May again (Figure 6.1).

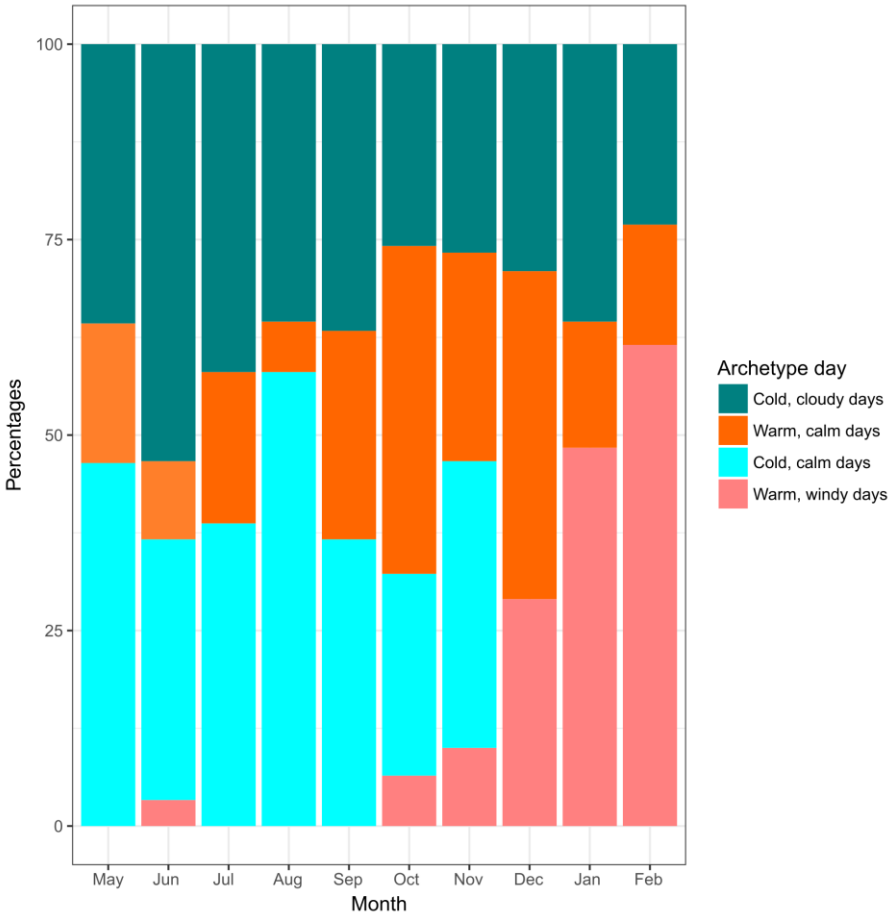

Figure 6.1 Percentage of each diurnal archetype, as defined in chapter 5, represented in each month throughout the seasons.

The GDD was determined for three different base line temperatures, which included 0, 5 and 10°C. Average daily temperatures rarely dropped below 10°C and the GDD increases linearly with time at a base line temperature of 10°C (Figure 6.2). The GDD with base line temperatures of 0 and 5°C, show that there is an increase in days above these temperature thresholds during the summer months of November until March (Figure 6.2).

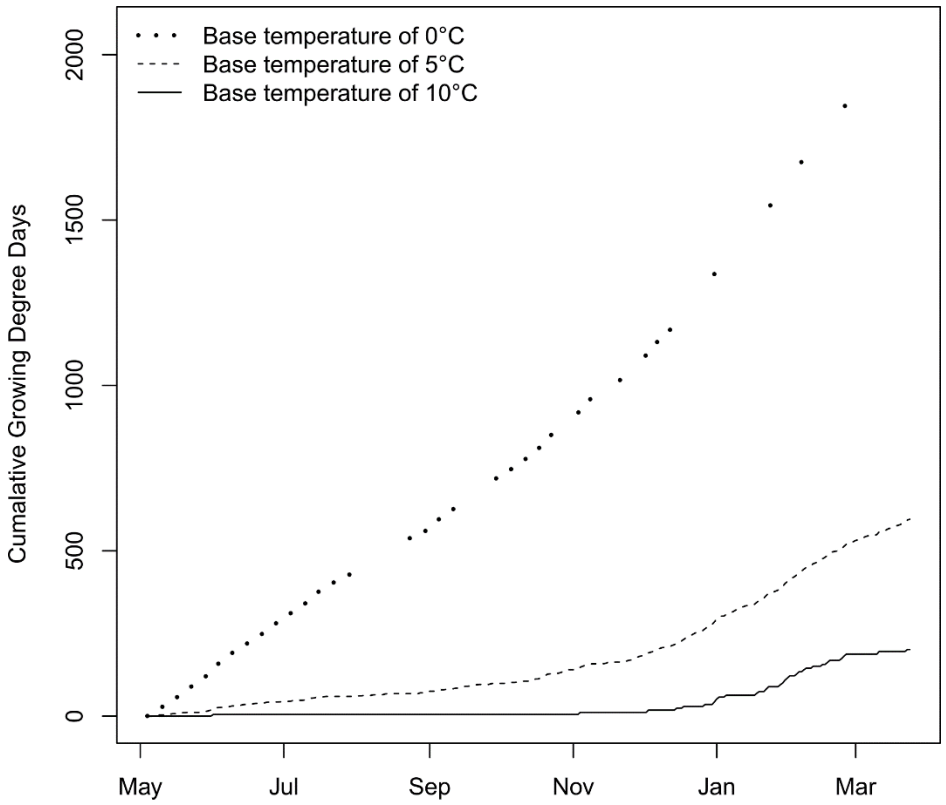

Figure 6.2 Cumulative GDD at three different base temperatures as measured on Marion Island for 2016-2017.

The peak number of stress days per month (based on soil water), indicated that the most moisture stress was experienced during August and January to February, irrespective of the soil water thresholds used (Figure 6.3).

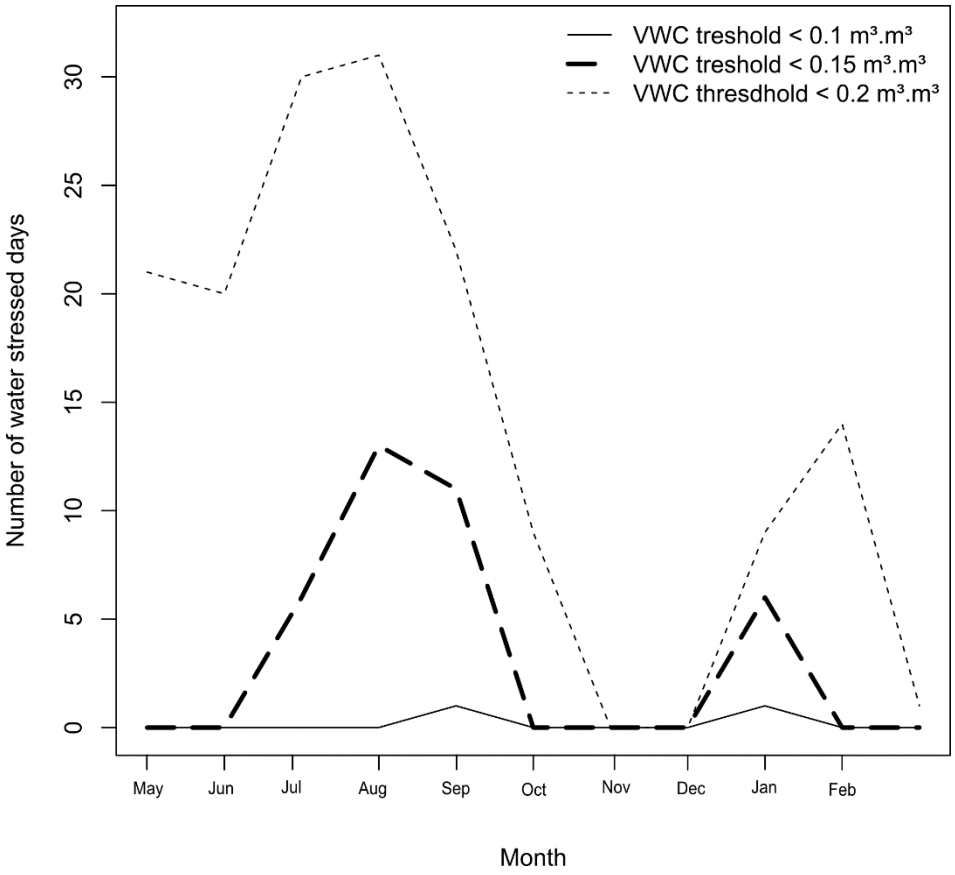

Figure 6.3 Number of days per month where soil water was below a certain threshold.

6.4.2. Seasonal trends of plant stress

From visual inspection of the seasonal PRI trends it seems that there was a decrease seen in average daily PRI measurements for both cushion plants during the "summer" months (Figure 6.4 – 6.5). Although there was an overall negative trend seen of PRI measurements during the "summer" months, PRI measurements for both *A. selago* and *S. procumbus* are highly variable throughout the seasons (Figure 6.4 – 6.5).

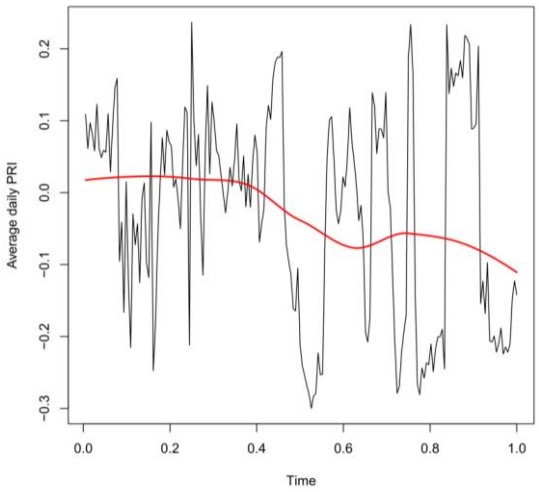

Figure 6.4 PRI trend of *A. selago* throughout the season. Duration of annual cycle observed (days) is scaled to 1 with May being the first month of measurements. Loess smooth is fitted.

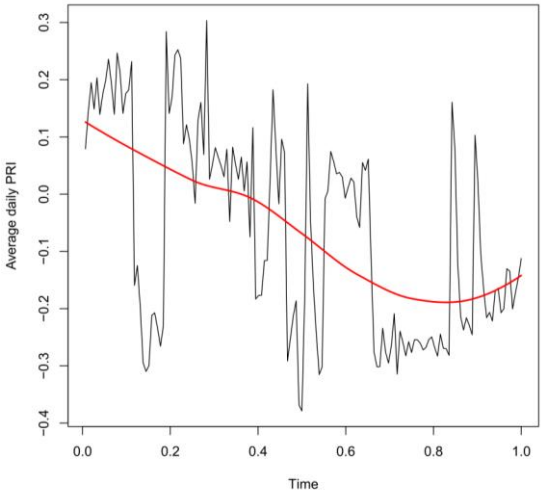

Figure 6.5 PRI trend of *S. procumbus* throughout the season. Duration of annual cycle observed (days) is scaled to 1 with May being the first month of measurements. Loess smooth is fitted.

There was an increase seen in average daily PRI measurements for both graminoids during the summer months (Figure 6.6 – 6.7).

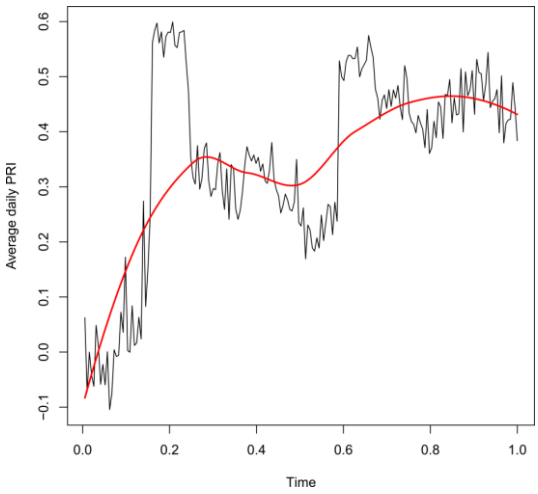

Figure 6.6 PRI trend of *A. magellanica* throughout the season. Duration of annual cycle observed (days) is scaled to 1 with May being the first month of measurements. Loess smooth is fitted.

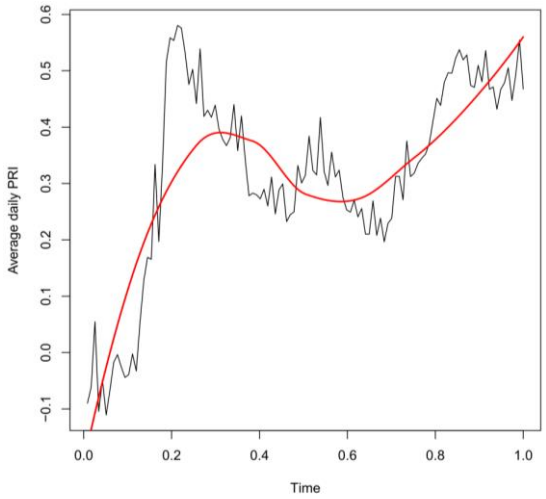

Figure 6.7 PRI trend of *A. stolonifera* throughout the season. Duration of annual cycle observed (days) is scaled to 1 with May being the first month of measurements. Loess smooth is fitted.

There was no trend in PRI measurements seen for *R. lanuginosum* during the year. Even though there was no trend seen in PRI measurements seen for *R. lanuginosum*, the PRI measurements during the winter months are highly variable with a slight decrease in PRI measurements during the "summer" months (Figure 6.8 – 6.9). A similar trend pattern of PRI measurements can be seen for *S. colerata* as for *R. lanuginosum.*

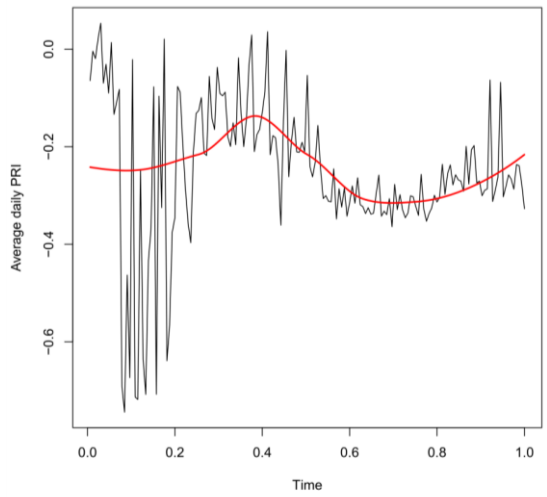

Figure 6.8 PRI trend of *R. lanuginosum* throughout the season. Duration of annual cycle observed (days) is scaled to 1 with May being the first month of measurements. Loess smooth is fitted.

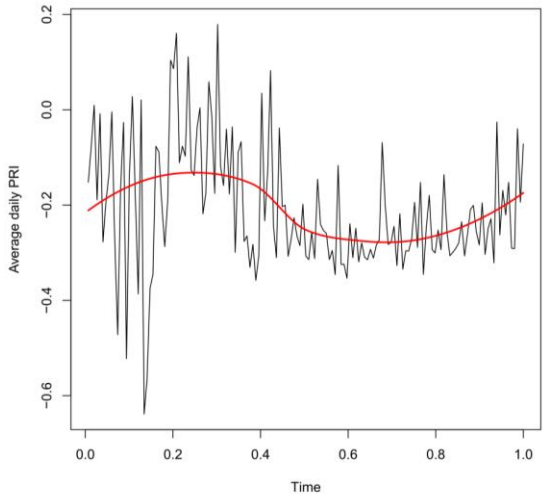

Figure 6.9 PRI trend of *S. colerata* throughout the season. Duration of annual cycle observed (days) is scaled to 1 with May being the first month of measurements. Loess smooth is fitted.

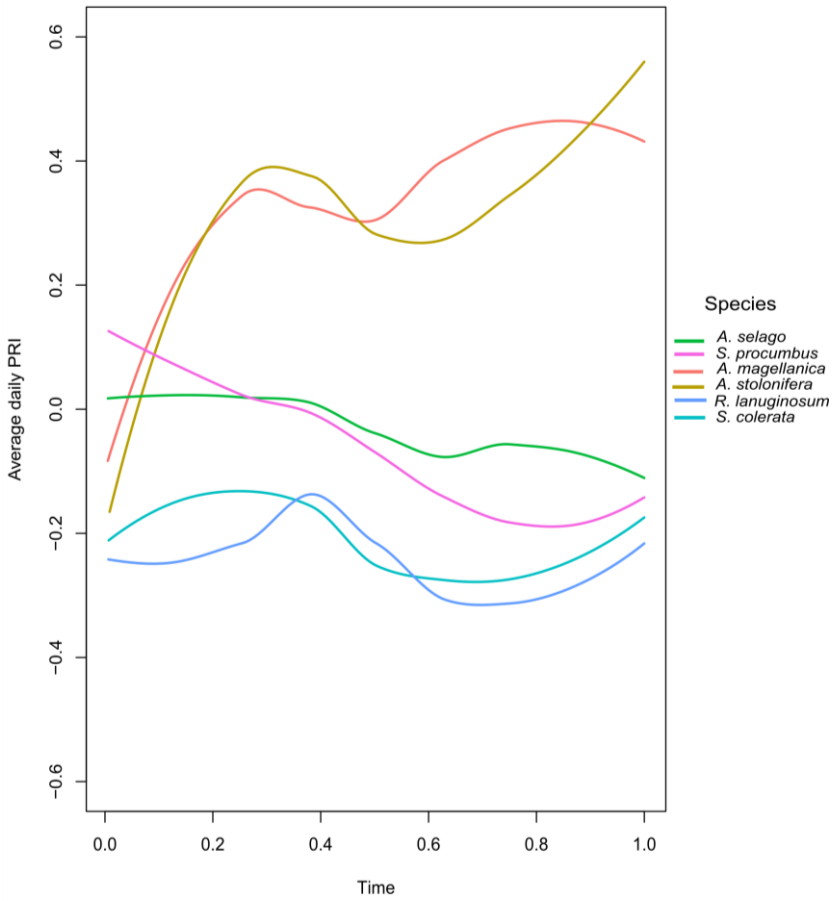

Figure 6.10 PRI trends of all species across seasons.

There was no correlation between chlorophyll content and PRI measurements throughout the seasons for all species (Table 6.1).

Table 6.1 Relationship between PRI measurements and chlorophyll content throughout the seasons for all species.

Cushion plants				
Species	**R^2**	**F**	**p**	**df**
A. selago	0.009	0.087	>0.05	10
S. procumbus	0.007	0.065	>0.05	9
Graminoids				
Species	**R^2**	**F**	**p**	**df**
A. magellanica	0.007	0.066	>0.05	10
A. stolonifera	0.168	1.008	>0.05	6
Lower plants				
Species	**R^2**	**F**	**p**	**df**
R. lanuginosum	0.047	0.490	>0.05	10
S. colerata	0.034	0.285	>0.05	8

The chlorophyll content was relatively constant throughout the year for all species, with the lower plant species having the lowest chlorophyll content as depicted in Figure 6.11.

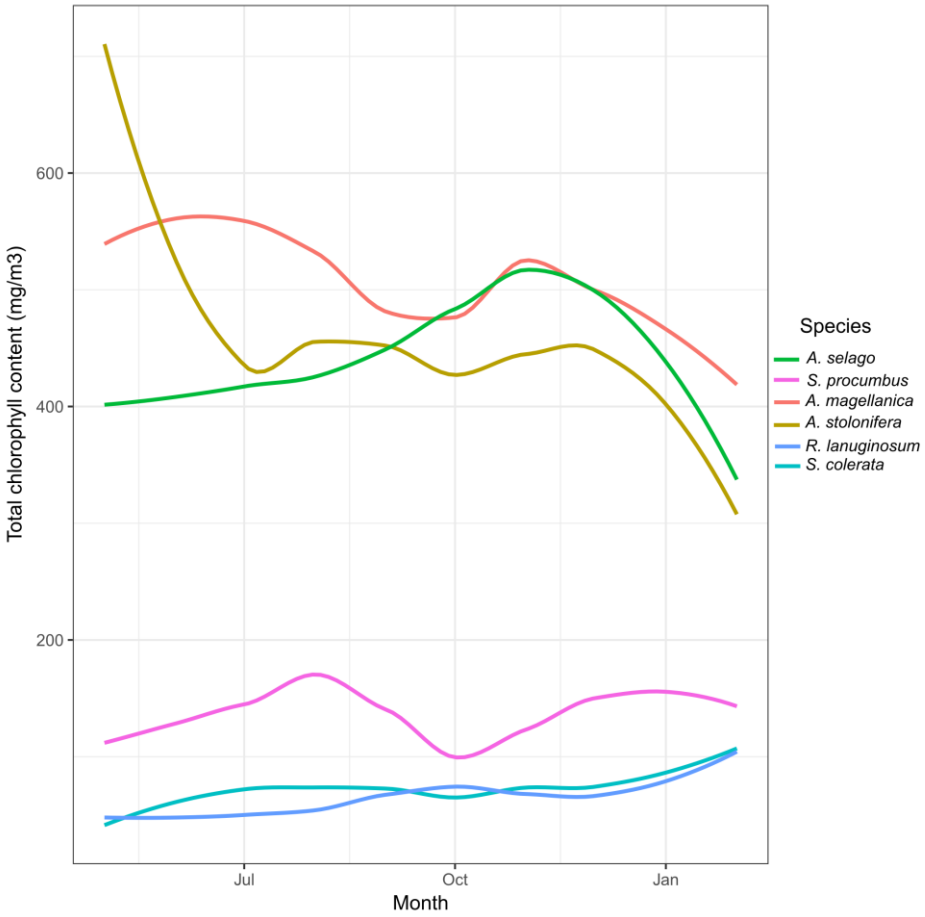

Figure 6.11 Change in chlorophyll content as measured by the CCM-300 throughout the study period. Measurements were made everyf 2 weeks. Loess smooth is fitted.

As shown in the chapter 4, PRI measurements correlated with other measurements of photosynthetic efficiency and stress, such as NPQ and Fv/Fm. From visual inspection it is clear that even though there are slight differences, the general trend of Fv/Fm measurements mimics the PRI measurements across seasons (Figures 6.12 – 6.15). Unfortunately due to the nature of these measurements, measurements could only be done during warm dry days and therefore sampling could only have been done in selected months. Problems were also experienced with taking fluorescence measurements of the lower plant species and reliable fluorescence measurements could not be taken.

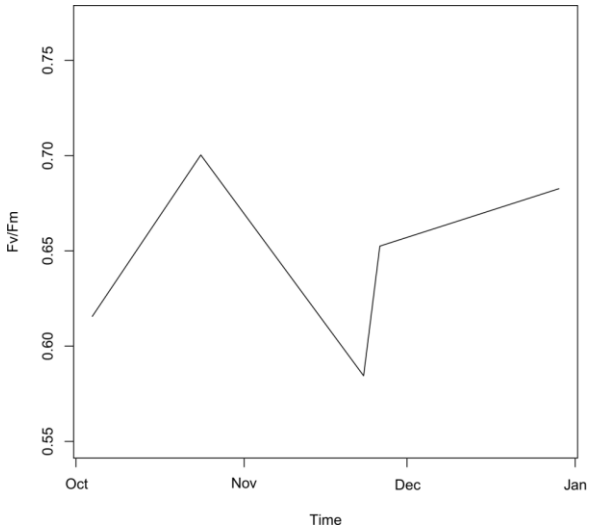

Figure 6.12 The average Fv/Fm of multiple leaves measured of *A. selago* throughout the season.

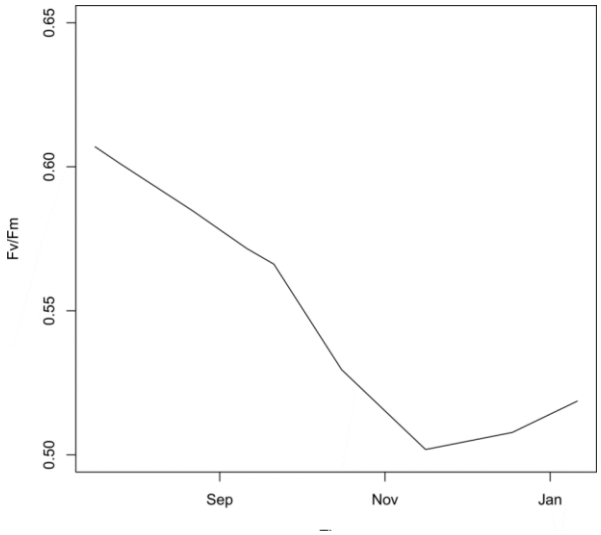

Figure 6.13 The average Fv/Fm of multiple leaves measured of *S. procumbus* throughout the season.

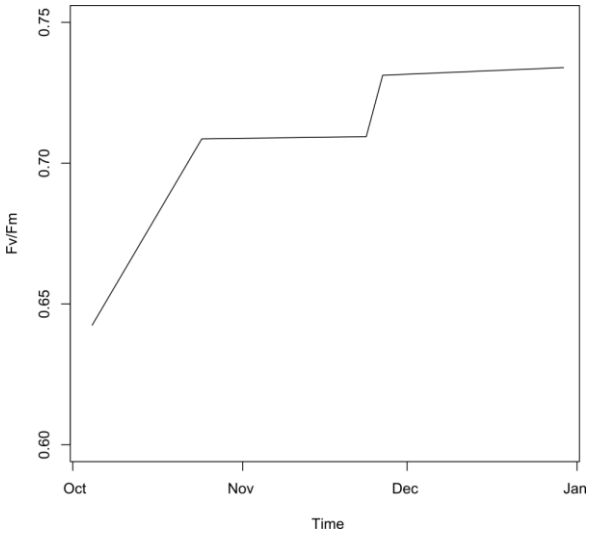

Figure 6.14 The average Fv/Fm of multiple leaves measured of A. magellanica throughout the season.

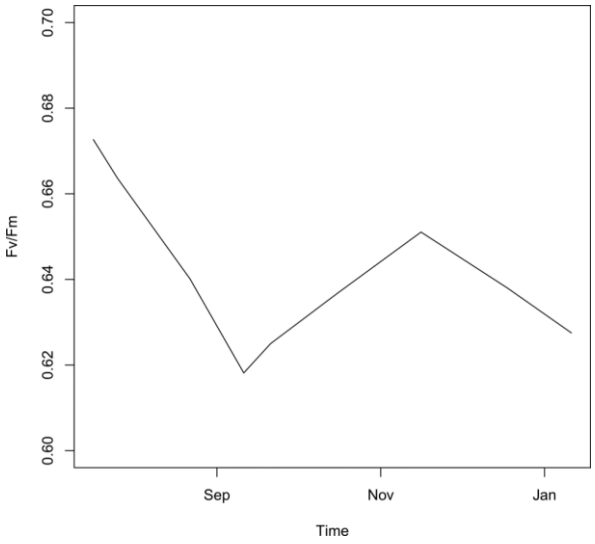

Figure 6.15 The average Fv/Fm of multiple leaves measured of A. stolonifera throughout the season.

6.4.3. *Seasonal environmental drivers of vegetation indexes*

To understand how environmental variables interact and drive changes in PRI and canopy temperature measurements throughout the season, AIC values were used to determine the model of best fit. Twenty four (24) different models were included in the analysis based on different combinations of variables. The same models were used to determine seasonal drivers, as what was used to determine diurnal drivers in the previous chapter. A general overview of models of best each species is given in Table 6.2.

The model of best fit driving seasonal PRI measurements for *A. selago* was air temperature and solar irradiance. The combination of environmental drivers influencing PRI measurements for *S. procumbus* was air temperature and VPD (Table 6.2).

The model of best fit influencing seasonal PRI measurements for *A. magellanica* was air temperature and soil water. The model of best fit influencing seasonal PRI measurements for *A. stolonifera* was wind speed and VPD (Table 6.2).

The model of best fit driving PRI measurements of *R. lanuginosum* is relative humidity. The combination of environmental variables influencing seasonal PRI patterns for *S. colerata* was air temperature and VPD (Table 6.2).

Table 6.2 GAM model section influencing PRI measurements of all species through the season. Logliks (loglikelihood), K (number of parameters), w_i (Akaike weight value), AIC (the AIC value).

Species	Models	Logliks	K	w_i	AIC
	Cushion plants				
A. selago	Air temperature + Solar irradiance	-230.372	4	0.993	-22.3724
S. procumbus	Air temperature + VPD	-121.216	4	0.926	-120.490
	Grasses				
A. magellanica	Air temperature +Soil water	-161.872	4	0.842	-153.87
A. stolonifera	Wind speed + VPD	-99.889	5	0.310	-93.967
	Lower plants				
R. lanuginosum	Relative humidity	-149.373	3	0.491	-180.3064
S. colerata	Air temperature + VPD	-156.145	4	0.316	-254.836

The relationship between environmental variables and vegetation indexes on a seasonal scale

Table 6.3 gives a general overview of the relationship between vegetation indexes (PRI and canopy temperatures) and environmental variables throughout the season. The correlations were done on mean daily values to understand the seasonal relationship within each species. Not all correlations will be discussed, but significant relationships of note will be reported.

Some of the significant relationships to note was the relationships between canopy temperatures and seasonal PRI measurements (Table 6.3). PRI measurements of the cushion plants and the lower plant species were significantly negatively correlated to canopy temperatures, with PRI measurements decreasing as canopy temperatures increased. Canopy temperatures of these groups significantly correlate with solar irradiance as well as air and soil temperatures. The inverse relationship between these variables and seasonal PRI

measurements for both the cushion plants and lower plants are seen (Table 6.3). The seasonal PRI measurements of both lower plants were significantly positively correlated to relative humidity (Table 6.3).

The seasonal PRI measurements of the graminoids were significantly positively correlated to canopy temperatures, with PRI measurements increasing as canopy temperatures increases. The seasonal PRI measurements of the graminoids were positively correlated with wind speeds as well as VPD measurements (Table 6.3). The seasonal PRI measurements of the graminoids were significantly positively correlated to soil water (Table 6.3).

Table 6.3 Correlation between PRI and canopy temperature and environmental variables throughout the season. Values represent Pearson correlation coefficient. (*= significant p-values) (T_{canopy} - canopy temperature, Solar – Solar irradiance, RH – Relative humidity, T_{air} – Air temperature, SVWC – Soil volumetric water content, T_{soil} – Soil temperature, kPa – Atmospheric pressure, wind – Wind speed, VPD – Vapour pressure deficit).

					A. selago					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.255***	0.077	0.216	-0.212	0.042	**-0.254***	-0.106	-0.044	-0.029
T_{canopy}	-	-	**0.490***	-0.043	**0.910***	0.025	**0.961***	-0.019	**0.487***	0.760
					S. procumbus					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.482***	**-0.264***	-0.051	**-0.353***	-0.104	**-0.507***	0.177	**-0.465***	**-0.051***
T_{canopy}	-	-	**0.525***	-0.049	**0.872***	0.001	**0.951***	-0.068	**0.511***	**0.764***
					A. magellanica					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**0.368***	0.165	0.074	**0.289***	**0.324***	**0.356***	-0.131	**0.401***	**0.318***
T_{canopy}	-	-	**0.432***	0.052	**0.915***	-0.049	**0.911***	-0.020	**0.531***	0.832
					A. stolonifera					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**0.322***	**0.237***	0.064	**0.282***	**-0.350***	**0.382***	-0.125	**0.376***	**0.064***
T_{canopy}	-	-	**0.397***	0.059	**0.892***	**0.241***	**0.951***	-0.065	**0.497***	**0.822***
					R. lanuginosum					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	-0.128	**-0.256***	**0.439***	**-0.212***	**0.239***	-0.029	0.017	-0.021	0.131
T_{canopy}	-	-	**0.465***	-0.032	**0.906***	0.002	**0.912***	-0.009	**0.327***	**-0.032***
					S. colerata					
	PRI	**T_{canopy}**	**Solar**	**RH**	**T_{air}**	**SVWC**	**T_{soil}**	**kPa**	**wind**	**VPD**
PRI	-	**-0.263***	**-0.638***	**0.532***	**-0.335***	0.049	**-0.215***	0.084	-0.098	0.121
T_{canopy}	-	-	**0.537***	-0.097	**0.934***	**0.274***	**0.976***	0.002	**0.428***	**-0.097***

6.5.Discussion

6.5.1. PRI as an indicator of seasonal photosynthetic capacity

PRI has been widely used to track diurnal changes in physiology (Gamon *et al.* 1997; Stylinski et al. 2002; Gamon *et al.* 2015). Physiological changes occurring throughout the growing season however are often not captured in studies conducted over small timescales (Stylinski *et al.* 2002). PRI measurements made over multiple growing seasons can reveal different patterns compared to smaller temporal scales. PRI measured throughout the growing season are influenced not only by stress limiting production, but also changes in chlorophyll content and other pigments (Stylinski *et al.* 2002; Magney *et al.* 2016).

Various techniques have been developed in order to isolate the seasonal component of the PRI signal (Magney *et al.* 2016). One of the most common techniques used is to subtract steady state PRI measurements (early morning PRI measurement) before xanthophyll conversion has taken place from the measured PRI signal at the maximum xanthophyll inter-conversion (happening at peak solar irradiance levels) (Gamon and Berry, 2012; Magney *et al.* 2016). Due to the variability of the light environment on Marion Island, the maximum solar irradiance levels can happen at virtually any time during the day (Schulze, 1971). It is therefore difficult to determine both the maximum xanthophyll inter-conversion point as well as the steady state xanthophyll state. Daily averages of all PRI measurements where therefore determined and used in order to determine the seasonal component of the PRI signal.

Total chlorophyll content was not correlated to the seasonal PRI measurements for all species. This indicates that the chlorophyll content changes throughout the growing season did not affect the seasonal PRI measurements made. Changes in the chlorophyll and other carotenoid ratios, can influence PRI measurements relating to light dissipation, by slowly changing the physiological response of plants in relation to slow environmental changes through the season (like temperature changes during winter and summer) (Filella *et al.* 2009; Porcar-Castell *et al.* 2012).

With the ability of PRI measurements to detect changes in the chlorophyll carotenoid content, PRI can be used to determine the photosynthetic activation of plants through the growing season (Gamon *et al.* 2015).Even though seasonal PRI measurements are not correlated with chlorophyll ratios, Stylinski et al (2002) showed that both the xanthophyll cycle as well as the total chlorophyll pigments were correlated with the photosynthetic capacity and efficiency of plants during the growing season (Stylinski *et al.* 2002). Different strategies are used by plants to dissipate excessive light energy on both diurnal and seasonal scales. On a diurnal scale the

conversion of xanthophyll pigments is used to dissipate excessive light energy, and on a seasonal scale changes in other carotenoid pigments are used (Filella *et al.* 2009).

The PRI signal can be influenced by other carotenoid changes besides xanthophyll pigments. (Filella *et al.* 2009). The change in xanthophyll pigments and other carotenoids can make a contribution to a decrease in photosynthetic efficiency over the season. These influences can have implications for using seasonal PRI to measure only xanthophyll de-epoxidation, however seasonal PRI can still be a valuable indicator of photosynthetic efficiency over different seasons (Filella *et al.* 2009; Porcar-Castell *et al.* 2012). This indicates that PRI measurements of the canopy are still a valuable tool for measuring plant stress and photosynthetic rates throughout the growing season.

During this study little variation was seen in the chlorophyll content of all species throughout the season. It is therefore most likely that the PRI signal is a reflection of xanthophyll pigments changing in response to seasonal stress, and not the change in chlorophyll content. The PRI measurements were correlated to other measurements of stress and photosynthetic efficiency, adding to the idea that seasonal PRI measurements can be used to track seasonal stress and photosynthetic efficiency patterns within plants.

6.5.2. Seasonal response of PRI

There was a clear segregation in seasonal PRI responses between the different functional groups. This response seen contributes to the validation of using remote sensing to identify unique patterns of physiological responses throughout the season, since species of the same functional group was not under observation on the same dates, but rather alternated between weeks.

The PRI trend during the season for the cushion plants decreased during the summer months. Significant stress can be experienced, leading to decrease in photosynthetic capacity, when temperatures exceed the temperature optima of plants. *A. selago* has been shown to have a significant negative relationship between photosynthetic rates and temperature increases (le Roux *et al.* 2005). Temperature inhibition during summer months can therefore be experienced during warmer months, leading to a decrease in carbon assimilation. Reduced light levels during periods of high temperature can therefore be beneficial for *A. selago*. It can be argued that cushion plants have a high photosynthetic rate during colder months, irrespective of solar irradiance increases. A similar pattern of PRI response was seen for *S. procumbus*, with an increase in light dissipation during the summer months.

There was a significant increase in PRI values of the grasses during the "summer" months. Both *Agrostis* species have high temperature optima ranging roughly between 10 - 20°C. Carbon assimilation rates for *Agrostis* species were found to not decrease significantly if temperatures drop slightly below the optimum temperature ranges, however they can decrease by 35% if temperature decreases below 0°C (Pammenter *et al.* 1986). The photosynthetic rate increases significantly with increased solar irradiance levels for both *Agrostis* species. The increase in photosynthetic rates during the "summer" months can therefore be attributed to the increase in solar irradiance levels during these months. Pammenter et al. (1986) showed that net carbon assimilation in the *Agrostis* species are rather attributed to the increase in light levels than the increase in temperatures on Marion Island (Pammenter *et al.* 1986).

There was no a significant trend seen in the PRI response of *R. lanuginosum*, however there was a significant negative trend seen in *S. colerata* during the "summer" months. The trend in *S. colerata* however is not as significant as the trend seen in other functional groups and might be a result of the high fluctuating PRI measurements during the "winter" months. *S. colerata* also measured a higher seasonal PRI range compared to *R. lanuginosum*. Both the lower plants have high fluctuating PRI response during the "winter" months with the PRI fluctuations decreasing during the "summer" months. The higher values of *S. colerata* seen during the "winter" months can be an indication of this plant having a higher photosynthetic capacity during the "winter" months (colder and wetter months).

Fluctuations in seasonal PRI measurements during different months can be seen in all species (excluding the seasonal overall trend). This can be indicative of environmental variation on a small scale effecting the PRI measurements of plants (Stylinksi *et al.* 2002).

Inspection of the change in frequency of diurnal archetypes (as defined in the previous chapter) during the seasons, can give some insight into how the seasons changes and give some understanding of how the seasons effects the PRI response of different functional groups. There was an increase in warm, windy days during the summer months with a decrease in cold and calm days. Cold days were experienced during all months, supporting the idea that cold temperatures can be experienced during virtually any season on Marion Island (Schulze, 1971). This seasonal change in climate seen can explain the trends seen in PRI measurements across seasons in all species.

The growing season for Marion Island has been proposed to be from mid-August until mid-June (Smith, 1987d), however this might not be the case for all functional groups found on the island. The increase in warm, windy days during October until February indicates that there is

an increase in more optimal temperatures during these months. This is reflected in the graminoid PRI measurements, with the grasses having increased photosynthetic efficiency during these months. The opposite trend is seen in the cushion plants, indicating that the optimal months for production for these plants might actually be during the colder months. The only functional groups that have a relatively steady state photosynthetic efficiency (based on the seasonal PRI measurements) are the lower plant species. Lower plant species have a lower photosynthetic rates, however production can take place at broad temperature ranges as well as under low light conditions and can therefore maintain long growing seasons (Russell, 1990). The main thing limiting production for bryophytes is changes hydrological regime found on the island (Russell, 1990). A decrease in seasonal PRI measurements is therefore expected during the drier "summer" months.

GDD only takes into account the temperature that is needed above which metabolic and physiological activity take place, however other environmental variables can have a significant effect on the growth and development of a plant (Idso *et al.* 1978). Water stress can have a significant effect on the growth of a plant, and inclusion of water stress in the GDD model will give a better understand physiological changes (Idso *et al.* 1978). On Marion Island little is known about the base line temperatures and water thresholds of different plant species. It is therefore difficult to combine these two concepts, especially since the physiological response of different plant species can be uniquely different. An approach was therefore taken to look at both these two concepts separately with multiple base line and water thresholds.

When looking at the GDD of different base temperatures, we can get an idea of the growing season on the island. GDD is often used to determine timing of phenology, growth and development of plants (Cleland *et al.* 2007). It is important to note however that GDD only takes into account temperature as a control for metabolic processes. When a base temperature of 5°C is used, we can see that there is an increase in accumulation of GDD during September continuing to March. When a base temperature of 10°C is used, this accumulation of GDD only starts during the month of January. The GDD with a base line temperature above 0°C accumulates linearly throughout the year, indicating that the average daily temperature on Marion Island rarely goes below 0°C. Since photosynthetic efficiencies of plants decreases drastically at temperatures below freezing point, it is unlikely that the GDD with a baseline of 0°C is an accurate description of the possible growing season on Marion Island (Pammenter *et al.* 1986; Russell, 1990). Based on the GDD with base

temperatures of 5 and 10°C, it can be assumed that the phenology changes seen in plants can be seen during the "summer" months on Marion Island (starting roughly mid-September).

When looking at the seasonal PRI response in relation to the GDD (with base temperatures of 5 and 10°C), the PRI response of grasses are correlated to the GDD trends. This can be indicative that the growing season is much shorter on Marion Island than previously thought, with changes in plant phenology beginning roughly mid-September. The exception to this, might be the lower plants where productions rates of below freezing point have been recorded on Marion Island (Russell, 1990).

Stress due to decreasing water can influence phenology and photosynthetic performance of plants. It is therefore important to look at stress days relating to water stress throughout the growing season (Idso *et al.* 1978). Substrate water content on Marion Island is high and is therefore not a limiting factor (especially along the coastal plains) (Schulze, 1971; Pammenter *et al.* 1986; Longton, 1988). Due to the high soil water levels measured on Marion Island, stress days were determined based on three different soil water thresholds. The number of stress days per month was higher during the winter months and then again during December until February. The stress day patterns correlates with the rain fall experienced each month (highest rainfall experienced in December). The number of water stress days can explain the variability in PRI measurements seen within the lower plant species during the winter months with lower plants being highly influenced by moisture regimes (Russell, 1990). Moisture stress can lead to high variability in PRI measurements as an indicator of photosynthetic efficiency. In water stress environments, a weak relationship can be seen between PS Ⅱ and the down regulation of photosynthesis (Stylinski *et al*. 2002).

6.5.3. Relationship of environmental variables and vegetation indexes through the season

The seasonal PRI pattern of different functional groups was correlated to different environmental variables over the season.

For cushion plants the change in temperature variables (canopy-, soil- and air temperature) had a significant negative effect on seasonal PRI measurements, with the plants experiencing significantly more stress as temperatures increased throughout the season. For both cushion plants increase in temperatures increased stress experienced by these plants. Increased temperatures can lead to a decrease in carbon assimilation in the temperatures exceed the temperature optimum (Sharkey, 2005). The PRI pattern and relationship with environmental

variables of cushion plants, gives the idea that optimum photosynthetic temperatures are experienced during the colder winter months on Marion Island.

Seasonal PRI measurements for *S. procumbus* were not only related to temperature variables, but also to variables controlling transpiration rates within the plant (VPD and wind speeds). In plants with high transpiration rates, leaf water potential can decrease with increases in VPD. This effect has been shown to increase in woody plants and can have a negative effect on photosynthetic efficiency and production. (Franks and Farquhar, 1999; Turner *et al.* 2017). Increased wind speeds can lead to an increase in water loss and coupling this with high transpiration rates can lead to increased stress on the plant (Smith and Steenkamp, 2001).

Seasonal PRI measurements for both grasses were positively correlated to temperature variables as well as variables influencing transpiration rates (VPD and wind). Both grasses have high temperature optima. The positive effect of temperature is therefore seen in both grasses, when seasonal temperature increases to more optimum temperature during the "summer" months (Pammenter *et al.* 1986). Both *A. magellanica* and *A. stolonifera* have the potential for high transpiration rates (Pammenter *et al.* 1986). With sufficient water content on the island, increased transpiration rates can therefore also lead to increase in production and photosynthetic efficiency during the "summer" (Franks and Farquhar, 1999).

The importance of moisture regimes in seasonal PRI patterns were evident in the lower plant species, with stress increasing with variables that lead to habitat moisture loss and drying. Lower plants were also positively correlated to soil water content, with seasonal PRI measurements increasing with an increase in soil water throughout the season. Lower plants are highly influenced by moisture regimes (Russell, 1990). The positive relationship between relative humidity as well as soil water can be seen and seasonal PRI measurements in the lower plants can be seen. *R. lanuginosum* seems to be more sensitive to soil water regimes compared to *S. colerata*. Increased temperatures, as well as solar irradiance, can lead to increased desiccation rates of lower plants and can increase stress significantly in lower plants (Russell, 1990). During the "summer" months increased temperatures, solar irradiance levels coupled with a decrease in moisture regimes can lead to decreased production rates (which is seen in lower plants).

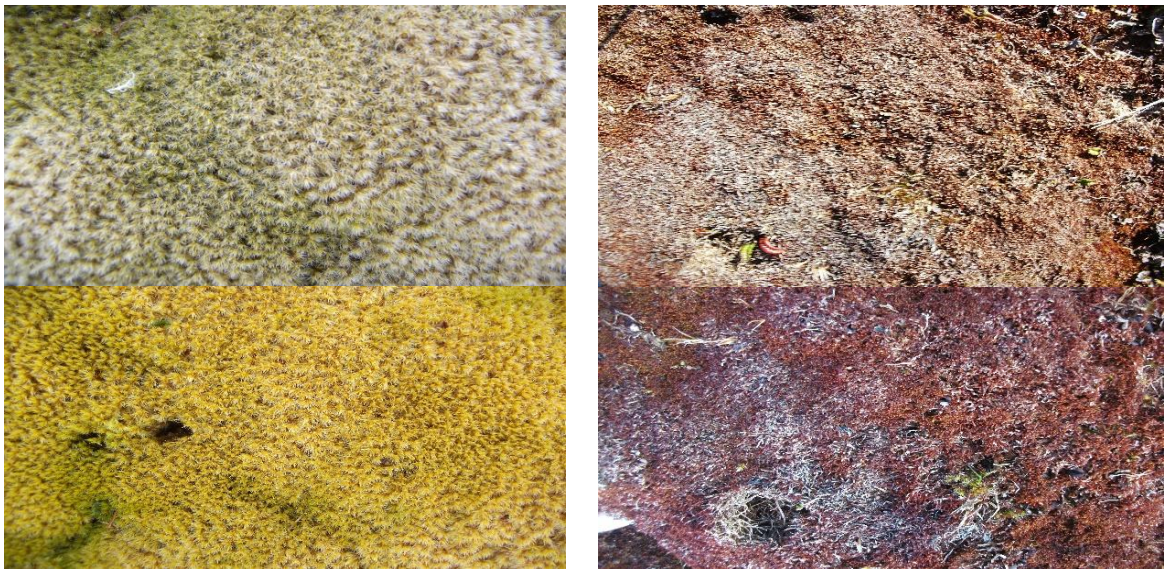

Image 6.1 Effect of desiccation (top photos) and increased moisture (bottom photos) of lower plants. Left*: R. lanuginosum*; Right: *S. colerata*

6.5.4. *Seasonal environmental drivers of diurnal physiological patterns*

The relationships between environmental variables and seasonal PRI measurements are reflected in the driver selection for the different functional groups. By using a multi-parameter approach to determine environmental drivers, it is possible to tease apart the interactive effects of variables and how they affect both stress (see Figures 6.1 and 6.2 for canopy visual responses to dessicvation stress) and photosynthetic efficiency throughout the season (le Roux *et al.* 2005).

Driver selection for the species was different within and between functional groups. This highlights the importance of diversity in responses to various environmental drivers, especially on a seasonal scale.

There were distinct PRI patterns seen between the different functional groups. On closer inspection it is clear that there is variation in the PRI response between species of the same functional group, even though the general trends are similar. This is indicative that there are different drivers for the different species, with some overlap within each plant functional group.

The importance of temperature as a driver for seasonal PRI patterns in both cushion plants is evident. Increased temperatures during the summer months can lead to stress if these temperatures exceed the temperature optimum of these plants (Valladares, 2003). The importance of VPD as a driver is also highlighted in the driver selection for *S. procumbus*. Increased VPD can lead to an increase in water loss. Loss of water due to transpiration can be minimised by effective water conduction elements (xylem), however when habitat moisture

is decreased, increased water loss due to higher transpiration rates and VPD can be negative (Demmig-Adams and Adams 1996; Franks and Farquhar, 1999).

Image 6.2 Comparison of leaf production of *A. magellanica* (left) and *A. stolonifera* (right) during the "winter" (top photos) and "summer" (bottom photos)

Driver selection for seasonal PRI measurements for grasses was variables influencing temperature and water loss (either through habitat moisture or through transpiration). Both *A. magellanica* and *A. stolonifera* have a high temperature optimum (Pammenter *et al.* 1986). Increases in temperature during the summer months would therefore decrease stress inferred from the PRI measurements. For *A. stolonifera* the importance of variables influencing transpiration rates during the "summer" months can be seen. Both grasses have a potential for high transpiration rates, however this is limited to efficient water availability (Pammenter *et al.* 1986). High productivities in herbaceous plants are coupled to increases in water loss (Franks and Farquhar, 1999). *A. stolonifera* has a high leaf turnover rate, with significant increases in canopy cover during the summer months (Pammenter *et al.* 1986). The importance of moisture loss in *A. stolonifera* gets highlighted with both VPD and wind being main drivers of stress during the seasons. The combination of wind speeds and VPD can decreases photosynthetic efficiency in *A. stolonfera* by increasing water loss (Pammenter *et al.* 1986). During periods of moisture stress a decrease in seasonal PRI measurements can therefore be observed.

Moisture regimes are an important driver for lower plant species. Lower plants lack proper water conducting elements and are therefore susceptible to desiccation. Production rates of *R. lanuginosum* are low and decreases in habitat moisture (especially) during the "summer"

months can lead to a decrease in production rates (Russell, 1990; Valladares, 2003). Relative humidity was the main driver for *R. lanuginosum* highlighting the important of a moisture rich environment to prevent desiccation for this species (Russell, 1990). Increases in air temperature and VPD can lead to increases in water loss. High desiccation rates are often seen with increased temperatures and solar irradiance in lower plant species (Russell, 1990; Franks and Farquhar, 1999, Valladares, 2003). Strong correlations between stress and habitat moisture levels in lower plant species have been recorded at other sub-Antarctic island and this study again highlights the importance of moisture regimes and environmental variables influencing moisture regimes on a seasonal scale for both *R. lanuginosum* and *S. collerata* (Russell, 1990). Lower plants on Marion Island have a very shallow "pseudo-root" system. Changes in soil water, other than surface moisture are often not accessible to these plants. The importance of moisture within the air therefore is highlighted as a source of habitat moisture, especially in *R. lanuginosum*. The lack of effective water conduction elements can lead to an increase in water loss, which is seen as VPD increases. The importance of water loss in *S. colerata* is revealed by the data, although this is not seen for *R. lanuginosum*. This could be attributed to the structural differences of these plants, with *R. lanuginosum* forming a type of "cushion" which decreases the leaf area that is exposed to the surrounding atmosphere.

6.6. Conclusions

The estimated growing season on Marion Island cannot be smply characterized as a "slow and steady" pattern, as has been previously indicated. Even though seasons cannot be clearly defined on the island, a shift in climate can be seen between the "winter" and "summer" months showing optimum growing seasons for different PFTs. These optimum growing conditions can vary to some degree within PFTs, but there are good indications that there are distinct differences between PFTs that reflect their structure and function. On closer inspection it is clear that there is variation in the PRI response between species of the same functional group, even though the general trends are similar. This is indicative that there are different drivers for the different species, with some overlap within each plant functional group.

Shifts in climate during the seasons were seen to differentially affect different PFTs. With climate regimes shifting on Marion Island due to climate change, it is important to understand how the shifts in seasons affect the production and growth of plants, since future shifts in climate can severely impact the production rates of plants.

7. Conclusion: Emerging findings and suggested further study

Measured production rates are much lower than the estimated rates for Marion Island (Lieth, 1973; Smith 1987a, b, c, d). Although various environmental variables has been proposed to be the limiting factors of production, few have been tested with *in situ* field measurements. Changes in environmental variables and climate can have a significant effect in on plant production, since it can have a significant impact on stress experienced by plants.

This study showed that the climate on Marion Island is highly variable across different timescales. The climate has been previously describe as stable with muted seasonal changes (Schulze, 1971). The study highlighted the importance to define the climate of Marion Island not only on seasonal or monthly scales, but also on sub-seasonal scales. The variability of the climate creates a challenging environment for optimal photosynthesis with plants not always being able to adapt to the changes. This significantly effects photosynthetic and production rates, since significant stress can be experienced if plants cannot adapt to environmental variability. During this study a clear difference in physiological responses was seen to environmental variables between different plant functional types.

Low levels of incoming solar irradiance have been proposed as one of the main factors limiting production due to the presence of cloud cover (Schulze, 1971). High variability in solar irradiance levels were observed on the island, with burst of high levels of solar irradiance seen for short periods of time during the day. It can be proposed that it is not necessarily the low levels of solar irradiance limiting plant production, but rather the high variability seen in the light environment, creating a highly stressful environment for plants to adapt to. Significant stress can be experienced if the incoming solar energy cannot be utilized.

Production models, based on annual temperature experienced on the island, estimated high rates of production (Lieth, 1973). Even though annual temperature experienced are higher than in northern Tundra systems, the temperature environment on Marion Island is not as stable with high diurnal temperature ranges seen. The response of plants to different temperatures were varied, with cushion plants and lower plants experiencing significant stress with increased temperatures compared to the grass species.

Both the positive and negative role of wind was seen where wind either helped to decrease canopy temperatures on days where the air temperature exceeded the temperature optimum of plants, or where wind increased water loss in plants. The role of wind can therefore vary depending on the type of day (warm or cold day) that was seen on the island. The importance

of moisture regimes influencing the production rates of lower plant species was once again highlighted during this study (Russell, 1990).

The growing season on Marion Island has been proposed to commence from middle of August and terminate near the middle of June, due to more ideal temperatures experienced during this period (Smith, 1987d). Inspecting the GDD data with different base temperatures, there is a clear shift in growing seasons based on temperature from November until April. This is much shorter than previously proposed. The seasonal response of different plants however varied, with stress experienced increasing significantly in cushion plants during these months. This could be a reflection of the increased temperatures, since the cushion plants experienced significantly less stress in colder temperatures. For both grass species PRI patters mimicked the GDD model, since they have high temperature optimuma. The lower plant species seem to be the only plant that followed the proposed long growing season, where a relatively steady state trend of photosynthetic efficiency was seen through the year (even though high variability was seen on smaller time scales). The stress experienced by lower plants however was significantly higher than any other plant functional group, with the lowest PRI values measured.

Seasons could not be clearly defined, however, shifts in climate were apparent between what can be identified as “winter” and “summer” months, showing different optimum growing conditions for plants. These shifts in climate can effect species and functional groups differently, with the shifts in climate during the seasons affecting different plant functional types differently. There was a clear differrentiation in response seen between different functional groups. The high variability of responses between different functional groups and species, highlights the fact that general assumptions about seasonal and diurnal drivers of stress and photosynthetic patterns cannot be made about all plants on Marion Island. Not only is annual measures of environmental variables important for predicting production rates, but high variability in environmental variables can cause significant stress on plants and decrease photosynthetic efficiency and production rates.

The use of PRI as a measure of physiological changes and stress shows promise for determining production patterns and what influences them, especially when these measurements are coupled with other meteorological and environmental measurements. This study showed that the use of PRI on Marion Island can be a valuable tool to determine stress and physiological patterns. The effectiveness of using single sites/canopies as a representation of other individuals in the same area was shown, since single replication is often the case with

remote sensing due to the cost of this technique. The study the focused on patterns and trends of physiological change and stress over time.

PRI can be a useful tool in exploring physiological changes of stress within a plant, however estimations of production cannot be solely made from only PRI measurements (Gamon *et al.* 1997). To do this a measurement of light absorption by plant canopies is required. NDVI measurements can supplement PRI measurements in order to determine estimations of production. NDVI can be used to determine light use efficiencies, which can give an indication of the amount of light that was absorbed by canopies (Gamon *et al.* 1992). PRI can be used to determine photosynthetic efficiency of absorbed light (Gamon *et al.* 2015). By combining these two measurements a credible estimation can be made of the production of observed vegetation. This would be extremely useful in isolated areas where in-field measures of production are difficult, or if the size of area is too large to sample.

PRI measurements correlate with other measures of photosynthetic efficiency and stress, however the strength of this relationship varies between species (Gamon *et al.* 1997). Inter-species comparisons of PRI measurements are therefore not possible and focus should rather be given to trends within PRI measurements within the same species over time. Increasing the replication of PRI measurements in the field can therefore be valuable to determine trends within the same species over time. However the use of this technique is expensive and replication over area is often not possible.

The increasing interest in deploying spectral reflectance sensors in the field for longer periods of time has led to the development of new inexpensive sensors. Few studies have focused on comparing different sensors and discrepancies between measurements by different sensors can arise. This can be due to different sensor configurations or difference of deployment of these sensors in the field (Harris *et al.* 2014; Gamon *et al.* 2015). It is therefore difficult to compare PRI measurements across different studies, however these measurements can still be a valuable indicator of physiological changes within plants (Harris *et al*. 2014).

Comparing PRI measurements to measured production values can be useful to better interpret the effect of stress on production. Differences in productions rates across communities on Marion Island have been observed (Smith 1987a, b, c, d). By understanding the photosynthetic rates of different plants species, we can estimate photosynthetic efficiency and production of plant communities that can be useful to determine annual production on the Island. Future research should therefore be given to measuring photosynthetic efficiency of

other plant species on the island, since this study focused only on selective plant functional types and species which is not representative of all species.

Temperature increases on Marion Island are seen to be occurring at higher rates than average global warming rates (Smith and Steenkamp, 1990; Bergstrom and Chown, 1999). The ice cap as well as the permanent snowline has disappeared on Marion Island (Sumner *et al.* 2004). These changes in climate have had a significant effect on the physical and the biotic components of the island. Shifts in climate can be seen in vegetation structure, distribution ranges as well as productivity rates (Chown and Smith, 1993; le Roux and McGeoch, 2008). By understanding how plants respond to environmental variables on a diurnal and seasonal scale, it will be possible to obtain a far more detailed picture of how plants will respond to changes in climate. With the current climate trends continuing, significant changes will be seen in the ecology of Marion Island. It is important to understand how the shifts in seasons affect the production and growth of plants, since future shifts in climate can severely impact the production rates of plants. The techniques described in this thesis would provide an extremely valuable set of tools to achieve this relatively inexpensively.

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